

COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

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OCE - LONG TERM ECOLOGICAL RESEARCH						
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TITLE OF PROPOSED PROJECT LTER: MCR II - Long-Term Dynamics of a Coral Reef Ecosystem						
REQUESTED AMOUNT		PROPOSED DURATION (1-60 MONTHS)		REQUESTED STARTING DATE		SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
\$ 5,640,000		72 months		09/01/10		
CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW						
<input type="checkbox"/> BEGINNING INVESTIGATOR (GPG I.G.2)			<input type="checkbox"/> HUMAN SUBJECTS (GPG II.D.7) Human Subjects Assurance Number _____			
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<input type="checkbox"/> PROPRIETARY & PRIVILEGED INFORMATION (GPG I.D, II.C.1.d)			<input type="checkbox"/> INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.j)			
<input type="checkbox"/> HISTORIC PLACES (GPG II.C.2.j)			_____			
<input type="checkbox"/> EAGER* (GPG II.D.2) <input type="checkbox"/> RAPID** (GPG II.D.1)			<input type="checkbox"/> HIGH RESOLUTION GRAPHICS/OTHER GRAPHICS WHERE EXACT COLOR REPRESENTATION IS REQUIRED FOR PROPER INTERPRETATION (GPG I.G.1)			
<input checked="" type="checkbox"/> VERTEBRATE ANIMALS (GPG II.D.6) IACUC App. Date 01/29/10						
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CERTIFICATION PAGE

Certification for Authorized Organizational Representative or Individual Applicant:

By signing and submitting this proposal, the Authorized Organizational Representative or Individual Applicant is: (1) certifying that statements made herein are true and complete to the best of his/her knowledge; and (2) agreeing to accept the obligation to comply with NSF award terms and conditions if an award is made as a result of this application. Further, the applicant is hereby providing certifications regarding debarment and suspension, drug-free workplace, lobbying activities (see below), responsible conduct of research, nondiscrimination, and flood hazard insurance (when applicable) as set forth in the NSF Proposal & Award Policies & Procedures Guide, Part I: the Grant Proposal Guide (GPG) (NSF 10-1). Willful provision of false information in this application and its supporting documents or in reports required under an ensuing award is a criminal offense (U. S. Code, Title 18, Section 1001).

Conflict of Interest Certification

In addition, if the applicant institution employs more than fifty persons, by electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative of the applicant institution is certifying that the institution has implemented a written and enforced conflict of interest policy that is consistent with the provisions of the NSF Proposal & Award Policies & Procedures Guide, Part II, Award & Administration Guide (AAG) Chapter IV.A; that to the best of his/her knowledge, all financial disclosures required by that conflict of interest policy have been made; and that all identified conflicts of interest will have been satisfactorily managed, reduced or eliminated prior to the institution's expenditure of any funds under the award, in accordance with the institution's conflict of interest policy. Conflicts which cannot be satisfactorily managed, reduced or eliminated must be disclosed to NSF.

Drug Free Work Place Certification

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative or Individual Applicant is providing the Drug Free Work Place Certification contained in Exhibit II-3 of the Grant Proposal Guide.

Debarment and Suspension Certification

(If answer "yes", please provide explanation.)

Is the organization or its principals presently debarred, suspended, proposed for debarment, declared ineligible, or voluntarily excluded from covered transactions by any Federal department or agency?

Yes ☐

No ☒

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative or Individual Applicant is providing the Debarment and Suspension Certification contained in Exhibit II-4 of the Grant Proposal Guide.

Certification Regarding Lobbying

The following certification is required for an award of a Federal contract, grant, or cooperative agreement exceeding \$100,000 and for an award of a Federal loan or a commitment providing for the United States to insure or guarantee a loan exceeding \$150,000.

Certification for Contracts, Grants, Loans and Cooperative Agreements

The undersigned certifies, to the best of his or her knowledge and belief, that:

- (1) No federal appropriated funds have been paid or will be paid, by or on behalf of the undersigned, to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with the awarding of any federal contract, the making of any Federal grant, the making of any Federal loan, the entering into of any cooperative agreement, and the extension, continuation, renewal, amendment, or modification of any Federal contract, grant, loan, or cooperative agreement.
- (2) If any funds other than Federal appropriated funds have been paid or will be paid to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with this Federal contract, grant, loan, or cooperative agreement, the undersigned shall complete and submit Standard Form-LLL, "Disclosure of Lobbying Activities," in accordance with its instructions.
- (3) The undersigned shall require that the language of this certification be included in the award documents for all subawards at all tiers including subcontracts, subgrants, and contracts under grants, loans, and cooperative agreements and that all subrecipients shall certify and disclose accordingly.

This certification is a material representation of fact upon which reliance was placed when this transaction was made or entered into. Submission of this certification is a prerequisite for making or entering into this transaction imposed by section 1352, Title 31, U.S. Code. Any person who fails to file the required certification shall be subject to a civil penalty of not less than \$10,000 and not more than \$100,000 for each such failure.

Certification Regarding Nondiscrimination

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative is providing the Certification Regarding Nondiscrimination contained in Exhibit II-6 of the Grant Proposal Guide.

Certification Regarding Flood Hazard Insurance

Two sections of the National Flood Insurance Act of 1968 (42 USC §4012a and §4106) bar Federal agencies from giving financial assistance for acquisition or construction purposes in any area identified by the Federal Emergency Management Agency (FEMA) as having special flood hazards unless the:

- (1) community in which that area is located participates in the national flood insurance program; and
- (2) building (and any related equipment) is covered by adequate flood insurance.

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative or Individual Applicant located in FEMA-designated special flood hazard areas is certifying that adequate flood insurance has been or will be obtained in the following situations:

- (1) for NSF grants for the construction of a building or facility, regardless of the dollar amount of the grant; and
- (2) for other NSF Grants when more than \$25,000 has been budgeted in the proposal for repair, alteration or improvement (construction) of a building or facility.

Certification Regarding Responsible Conduct of Research (RCR)

(This certification is not applicable to proposals for conferences, symposia, and workshops.)

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative of the applicant institution is certifying that, in accordance with the NSF Proposal & Award Policies & Procedures Guide, Part II, Award & Administration Guide (AAG) Chapter IV.B., the institution has a plan in place to provide appropriate training and oversight in the responsible and ethical conduct of research to undergraduates, graduate students and postdoctoral researchers who will be supported by NSF to conduct research.

The undersigned shall require that the language of this certification be included in any award documents for all subawards at all tiers.

AUTHORIZED ORGANIZATIONAL REPRESENTATIVE		SIGNATURE		DATE	
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* EAGER - Early-concept Grants for Exploratory Research

** RAPID - Grants for Rapid Response Research

PROJECT SUMMARY

Intellectual Merit: The Moorea Coral Reef (MCR) LTER is an interdisciplinary research and education program that was established in 2004, to explore the joint effects of climate and disturbance on the structure and function of coral reefs. Our study area is the reef complex that surrounds the island of Moorea in French Polynesia. Our initial focus (MCR I) was to advance understanding of major controls of processes that modulate ecosystem function, shape community structure and diversity, and determine abundance and dynamics of constituent populations. We build on this foundation by adapting a unifying conceptual framework (US LTER 2007) and developing a set of research themes to organize the MCR II research program and facilitate cross-site collaboration. Coral reef ecosystems appear especially vulnerable to changes in abiotic drivers associated with Global Climate Change (GCC). These arise from two mechanisms related to increasing concentrations of atmospheric CO₂: rising seawater temperature due to greenhouse warming, and changing seawater chemistry known as Ocean Acidification (OA). A paradigm shift occurred within the past decade regarding the relative importance of these climate-related drivers to coral reefs. The focus initially was on rising seawater temperature because it triggered several large-scale, conspicuous coral bleaching (i.e., loss of the endosymbiont *Symbiodinium*) events. There now is widespread recognition that OA and its interaction with rising temperature have the potential to cause even more sweeping changes. These drivers occur against a backdrop of other press (e.g., fishing) and pulse (e.g., storms) perturbations. During MCR I, a brief outbreak of crown-of-thorns seastars (COTS) resulted in the death of virtually all coral on the fore reef of Moorea, bringing issues related to state change, resilience (recovery), interactive effects and indirect cascades to the forefront. The fundamental question that we address in MCR II is:

How do drivers that operate over different spatial and temporal scales interact to influence the structure and function of coral reef ecosystems?

Our three organizing themes are: (i) interactive effects among drivers, (ii) indirect effects arising from structure – function linkages, and (iii) resilience and resistance in relation to structure – function feedbacks. The six goals of MCR II are to: (a) continue our long-term datasets on physical drivers, community dynamics and ecosystem processes; (b) maintain a long-term resilience experiment; (c) contribute to understanding of how Global Climate Change drivers will affect coral reefs and what factors influence resistance and resilience; (d) develop and test general ecological theory; (e) continue to improve our information management system to more fully meet the needs of the LTER network and broader scientific community; and (f) enhance our outreach components.

Broader Impacts: Coral reefs are not just ecologically important - they yield upwards of \$375 billion annually in goods and services (most of it in the developing world) that are vulnerable to human activities and climate forcing. Hence our research has relevance and application to resource managers, policy makers and stakeholders worldwide. Broader impacts arising from our educational activities include postdoctoral mentoring, research that integrates undergraduate and graduate training, progress towards an ethnically diverse MCR student community, active participation of K-12 teachers in MCR research, incorporation of MCR findings in teaching curricula, participation of MCR faculty and graduate students in the Three Seas Program, and involvement of faculty and students from predominately undergraduate and minority-serving institutions. Additional impacts are realized by our outreach efforts, including partnerships with three local schools that serve socio-economically disadvantaged and minority students, and with the Atitia Center on Moorea to reach Tahitians. While our information-rich web site will continue to be a primary outreach portal, we plan to develop a partnership with another web-based entity to target middle-school students.

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SECTION 1 - RESULTS FROM PRIOR SUPPORT

LTER: Long-Term Dynamics of a Coral Reef Ecosystem

Grant No: OCE0417412; Funding (2004-2010): \$4,860,209 (Excluding supplements)

The Moorea Coral Reef LTER (MCR LTER) is an interdisciplinary research and education program established in September 2004 to investigate the major controls over the dynamics of coral reefs and how they are influenced jointly by climate and disturbance. Its primary research objectives are to understand key processes in coral reef ecosystems that (1) modulate ecosystem function, (2) shape community structure and diversity, and (3) determine abundance and dynamics of constituent populations. The MCR site consists of the coral reefs surrounding the island of Moorea, French Polynesia, including three major reef habitats (fringing reef, back reef, fore reef) and two bays on the north shore (Fig. 1-1). Field operations are based at UC Berkeley's Gump South Pacific Research Station (<http://moorea.berkeley.edu/>). During MCR I, 18 postdoctoral investigators, 64 graduate students, 63 undergraduates, 53 technicians / programmers and 6 K-12 teachers have participated. To date, MCR scientists have produced 114 publications (Table S-1, Supplementary Documents) and given over 225 presentations.

RESEARCH

During the initial years of this funding period, MCR investigators and students self-assembled into four thematic working groups: (i) Time Series Measurements and Response of the Ecosystem to Perturbations, (ii) Coral Functional Biology, (iii) Bio-Physical Interactions and Coupling and (iv) Population and Community Dynamics. Many individuals are members of more than one group. Working group meetings have facilitated cross-disciplinary studies and promoted the inclusion of individuals of all educational stages into the project.

Spatially Explicit Time Series Program and Response of the System to

Perturbations: The goals of the time series program are to measure long-term trends in the physical environment and coral reef biota, provide a contextual basis for process-oriented studies and parameter values for modeling efforts, and meet the needs for comparative analyses within the LTER network. We established a time series program that includes measurement of a suite of relevant physical and biological variables. Depending on the taxon or process under investigation, the scale and scope of the measurements encompass a variable number of sites, zones, depths or frequencies of sampling. The most spatially inclusive sampling includes three habitat types at two locations on each of the three shores of Moorea (Fig. 1-1). Physical data collection (mainly by deployed oceanographic instruments) focuses on factors known to influence coral ecosystems, including temperature, light, nutrient availability and water flow. Salinity, turbidity, inorganic nutrients and the hydrographic structure and variability associated with the water column seaward of the reef sites are measured. Biotic sampling includes estimation of NPP of the reef community using a control volume technique and NPP of the water column using standard ¹⁴C tracer/bottle techniques. Abundances of benthic organisms (fish, algae, macroinvertebrates) are estimated by scuba divers along transects, and cover of coral and other sessile organisms is determined by analysis of high-resolution digital photographs. Importantly, the digital images provide an enduring archive from which additional data can be extracted. Zooplankton and microbial communities are assessed at north shore sites. Regional scale properties (e.g., sea surface temperature, sub-surface chl *a* concentration, sea surface height) are estimated via remote sensing using existing satellite sensors. Meteorological data come from our met station and from Météo France.

Coral reefs are subject to a variety of physical and biotic disturbances. In the early 1990s the reefs of Moorea were affected by several disturbances that significantly

reduced live coral cover (Adjeroud et al. 2009). After ~15 years of recovery that saw substantial increases in cover of coral (Fig. 1-2), a recent outbreak of crown-of-thorns seastars (COTS) reduced live coral on the fore reef from up to 50% to less than 10% cover (Fig. 1-2). This disturbance affords the opportunity to track responses of reef organisms to the near-complete loss of the foundational scleractinian corals. For example, our time series data show declines in fish species that associate with live branching coral, and increases in abundance of herbivorous fish that consume algae that grow on the dead coral substrate (Fig. 1-2). This major perturbation also is enabling us to study resilience (recovery), and in 2009, we initiated a long-term experiment to examine reef resilience following two kinds of pulse disturbances: loss of all coral structure from physical damage, and loss of tissue only from such disturbances as bleaching, disease or predation. Overfishing, a press driver, was crossed with each of the coral structure treatments.

Coral Functional Biology: A major research thrust has been to explore physiological responses to variation in key abiotic drivers of coral performance (temperature, light, aragonite saturation state [Ω_a]), with the objective of better understanding how corals will respond to global climate change (Edmunds 2008a, 2008b, 2009, Edmunds & Gates 2008, Putnam et al. 2008, Fitt et al. 2009, Muehllehner & Edmunds in press, Putnam & Edmunds in press). This work has included interspecific comparisons (Edmunds 2009) to identify taxa that are resistant to environmental challenges, and has addressed the role of oscillatory conditions in modifying responses of corals to physical stress (Putnam & Edmunds in review). We have focused on oscillatory conditions as the lagoon of Moorea has strong diurnal variation in seawater temperature, and in other locations (i.e., Taiwan), oscillatory thermal conditions are associated with reef resilience. Our work has identified massive *Porites* spp. as a coral that can resist environmental stress, and we are exploring the physiological and genetic basis of this characteristic. Interestingly, while this taxon benefits from acclimatization to low temperature, one sympatric congener (*P. irregularis*) has greatly reduced capacity for acclimatization when it subsequently is exposed to high temperatures (Edmunds 2009; Fig. 1-3). Analysis of *Symbiodinium* genotypes is characterizing the biological landscape within which these corals function and the possibility for changes in their symbionts to better tolerate the changing environment (Fig. 1-4).

A critical challenge we are facing as our process-oriented research advances is the need for integration among studies and biological processes, a task complicated by the non-linear interdependence of many coral traits, and their strong responses to a diversity of physical drivers. We have chosen Dynamic Energy Budgets (DEB) as a tool to achieve this integrative capacity, and have developed a DEB model for a symbiotic mixotroph (Fig. 1-5, Muller et al. 2009a, b) that specifies the flows of matter and energy among the host coral, its symbiont dinoflagellates (*Symbiodinium*) and the environment. Of particular value in this effort is the potential for DEB theory to explore the regulatory mechanisms needed to sustain the symbiotic relationship, and to serve as a construct with which meta-analyses of physiological studies can be completed (e.g., Osenberg et al. 1999); currently, we are exploring this capacity to evaluate the effects of ocean acidification (OA) on coral performance. In a parallel effort, population and evolutionary dynamics modeling of corals and their symbionts revealed that unless symbiont populations have variation in thermal tolerance, climate change likely will be too rapid for coral reef persistence into the next century (Baskett et al. 2009).

Bio-physical Interactions and Coupling: A central thesis of the MCR research program is that coral reefs are physically-forced systems, with effects that range across a broad continuum of spatial and temporal scales. Our understanding of one of the most important physical drivers - water movement - has increased dramatically during this grant period. For example, the offshore wave climate, which varies strongly both

spatially and seasonally (Fig. 1-6), drives circulation in the lagoons on Moorea (Fig. 1-7, Hench et al. 2008). Mesoscale sea level perturbations (MSLPs) produce low frequency (weeks) sea level changes around Moorea that could modulate effects of waves breaking and currents behind the reef crest (Fig. 1-8). Ecological processes in the lagoon that are mediated by flow could be affected by the action and interaction of these two physical drivers. Further, flow can interact with other physical and/or biological drivers to affect ecosystem function. For example, reef primary production on the north shore of Moorea is forced by variation in both light and water flow on several temporal scales. Tidal-related differences in hydrodynamics result in co-variation of light and flow during the day, centered on solar noon (Moorea is near an amphidromic point). While the majority of variation in reef Net Primary Production (NPP) is explained by light (not including extreme light variation due to clouds), during periods when light is greater than I_k (approximately $800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), at least 20% of the variation in NPP is explained by flow speed (Fig. 1-9). These light levels are present for 6 to 9 hours per day, suggesting that flow can have a modulating influence for much of the day. These results emphasize the importance of co-variation of environmental drivers in determining a key process of coral reef ecosystem function. Measurements of NPP on the back reef reveal values that generally fall within the range of NPP estimates for other Pacific coral reefs (about $5\text{-}20 \text{ gO}_2 \text{ m}^{-2} \text{ d}^{-1}$) but with a pattern of decreasing values over time (Fig. 1-10). It is not clear whether the reduction in metabolism is related to changes in community structure or to other biotic and/or abiotic drivers. Rates of nitrogen fixation on the back reef also are characteristic of Pacific back reef/reef flat values ($6\text{-}30 \mu\text{mol ethylene m}^{-2} \text{ d}^{-1}$, Williams & Carpenter 1997). Trends in the concentrations of dissolved nutrients in the water column closely mirror those in the oceanic water around Moorea (Fig. 1-11). About 80% of the variation in nutrients over the reefs can be explained by variation in nutrients offshore, a finding consistent with circulation models of the north shore which calculate water residence times on the back reef to be on the order of hours (Hench et al. 2008). A slight but consistent elevation of nutrient concentrations above oceanic waters at all reef and bay sites suggests that nutrient regeneration and input from land might generate the higher water column primary production observed in nearshore relative to offshore waters (Fig. 1-10).

Fish predation is an important means of sublethal damage to small corals in the lagoon at Moorea, and we have explored biophysical coupling among fish predation, flow and seawater temperature. Laboratory experiments revealed that the growth recovery of *Porites* damaged to a degree consistent with that caused by fishes was affected by water temperature but not flow speed; photophysiology outside the damaged area of the coral was influenced by temperature, flow and damage. This suggests recovery may vary among habitats as a function of flow and temperature regimes (Fig. 1-12, Edmunds & Lenihan 2009).

Population and Community Dynamics: Much MCR research has focused on host corals and their associated invertebrate and vertebrate species. Study of this model community enables the investigation of a range of species interactions as well as other processes such as benthic-pelagic coupling. Of course, the best-known mutualism on tropical reefs – the coral/*Symbiodinium* interaction – is central to the existence of the coral reef ecosystem and we are exploring the complex patterns of distribution of *Symbiodinium* and their coral hosts on Moorea. Additional mutualisms also involve corals. For example, trapeziid crabs shelter from predators and remove sediment from their host coral, which is imperative to the survival of corals in areas prone to sedimentation (Stewart et al. 2006). In a newly described mutualism; tube-forming amphipods associate with encrusting corals (*Montipora*) and cause long finger-like projections to form, providing shelter to the amphipods and protecting the coral from several predators (Bergsma 2009). Resident damselfishes subsidize growth of corals and anemones via provision of ammonium and other nutrients ultimately derived from

the plankton (Fig. 1-13, Holbrook & Schmitt 2005, Holbrook et al. 2008). The host-associated fish are providing an ideal system to explore biotic interactions such as indirect mutualism (Holbrook & Schmitt 2004) and intraguild predation (Schmitt et al. 2009) as well as the patterns and underlying mechanisms of density dependence (Schmitt & Holbrook 2007). We have a large ongoing study of a set of 66 patch reefs formed by large *Porites rus* colonies. The diversity and species composition of fishes hosted by these structures are related to both their size and structural complexity (Brooks et al. 2007), and they are linked to water column productivity via planktivory. The horizontal flux of zooplankton over the lagoon is positively related to flow velocity, but there is a considerable degree of depth stratification, a novel finding for such a shallow lagoon environment (Alldredge & King 2009). The distribution of zooplankton in this shallow water column may result from a combination of zooplankton behavior (upward swimming) and/or consumption by predators.

CROSS-SITE AND NETWORK ACTIVITIES

MCR personnel have been active in LTER Network activities, including membership on the LTER Executive Board, NISAC and on several Mid-term Review teams for LTER sites, presentation of talks at the LTER Symposium held at NSF each year, and co-editorship of the LTER DataBits. MCR investigators participated in the LTER decadal, ISSE and Network planning processes, and several have been involved in EcoTrends Working Groups. UC Santa Barbara is the lead campus for both the SBC and MCR LTER sites, providing opportunities for synergism as a total of 7 MCR investigators are participants in both projects. Cross-site activities include participation in each other's annual meetings and close collaboration in information management and development of web site tools. Examples of cross-site research projects include modeling of phase shifts in temperate rocky reef and coral reef ecosystems (Buenau et al. 2007), an exploration of the distribution and dynamics of DOM and its fate in temperate and tropical reef systems, and a socioeconomic project comparing management of fisheries. MCR LTER is collaborating with an international group, including other LTER (NTL, FCE, ARC, MCM) and ILTER sites (Kenting Coral Reef and Yuan Yang Lake, Taiwan), to develop sensor networks in coral reefs (CREON, <http://www.coralreefeon.org>) and lakes (GLEON, <http://www.gleon.org/>) and to promote network-level science. Major international partners for CREON are the Kenting Coral Reef ILTER site in Taiwan and the Australian Institute of Marine Science in Townsville, with cyberinfrastructure development led by groups at CalIT2 at UC San Diego and at the National Center for High Speed Computing in Hsinchu, Taiwan. Real-time meteorological and oceanographic data can be viewed on our web site. The MIRADA-LTERS project (<http://amarallab.mbl.edu/mirada/mirada.html>) did a Microbial Biodiversity Survey at aquatic LTER sites. MCR has worked closely with the MIRADA project to integrate MIRADA data into existing MCR-supported projects that investigate linkages between microbial community structure and coral reef ecosystem processes. We are also collaborating with the Moorea Biocode Project (<http://www.mooreabiocode.org/>) to test the efficacy of biocoding technology in studies of reef food webs.

INFORMATION MANAGEMENT

MCR LTER strives to meet the ever emerging and constantly changing challenges of organizing and preserving short- and long-term data sets in a format that facilitates their accessibility and analysis. MCR has adopted Metacat and EML as a primary information storage tool, rather than as just an exchange format. Our EML documents are contributed to NCEAS/LNO by replication or harvesting, depending on the compatibility of the participating Metacat installations. A list of LTER datasets and their documented online use are provided in Table S-2 (Supplementary Documents). A more complete description of how we manage our data is provided in Section 4. MCR data sets and metadata are online at <http://mcr.lternet.edu/data/index.html>.

DEVELOPMENT OF HUMAN RESOURCES, EDUCATION AND OUTREACH

Education activities include the training of undergraduate and graduate students and post-doctoral fellows. The focus at all three levels is to involve students directly in research activities, including those directly supporting LTER site research. Most conduct field work at the MCR site; some work mainly in campus laboratories. Students of all levels attend the annual two-day MCR All-Investigator Meeting, as well as other site activities, such as research seminars and the project's ongoing interdisciplinary working groups. We initiated a student and researcher exchange program with the Kenting Coral Reef ILTER site in Taiwan; to date 6 MCR graduate students, 1 postdoc and 6 MCR faculty investigators have conducted research projects at the NMMBA at the Kenting Coral Reef site, funded through programs at NSF (OISE, EAPSI, IRFP) and NSC Taiwan. MCR participates in campus initiatives to recruit graduate students from underrepresented groups and we have been successful in this regard. We integrate our research activities with undergraduate and graduate instruction through the Three Seas Program of Northeastern University, a year-long marine biology course with a 10-week academic quarter taught at the Gump Station in Moorea. Six MCR investigators have taught in the program, and several MCR graduate students serve as teaching assistants each year. One focus of our outreach efforts has been to develop web site resources such as our online encyclopedia with information, photos and video clips about organisms found in major reef habitats in Moorea. Another section features research pages for MCR graduate students, with photos and descriptions of their projects. A teacher resource section hosts K-12 teaching resources including lesson plans written by 4 teachers who have received RET supplements to engage in research at our site. Our school partnerships focus on a variety of schools, mostly those with large enrollments of underrepresented or economically disadvantaged groups, and include Isla Vista Elementary School (Santa Barbara), Carpinteria Middle School (Carpinteria), and Washington Accelerated School (Pasadena); we also work with select private schools including Milken Community High and Viewpoint Schools (both in Los Angeles). In all of our partner schools teachers use curricula based on MCR research. Fourth graders from Washington Accelerated School visit the coral reef exhibit that MCR sponsors at UCSB's REEF aquarium outreach facility. We celebrate Earth Day in Santa Barbara with an information booth about coral reefs targeted at young children. Outreach activities in Moorea include activities with the local association Te Pu 'Atiti'a, which along with the Gump Station pursues educational and research programs on biodiversity, traditional knowledge, culture, and the relationship between human societies and natural ecosystems.

SITE MANAGEMENT AND INSTITUTIONAL RELATIONS

The MCR is administered by the Marine Science Institute at UC Santa Barbara. Lead PI Schmitt serves as the project's primary point of contact with NSF, the LTER Network, campus administrative units, and UC Berkeley's Gump Station. Schmitt and three Co-Principal Investigators (Carpenter, Edmunds, Holbrook) oversee all operations. A half-time Deputy Director (Brooks) assists with day-to-day aspects of the project, and serves as the liaison between the project's investigators and the Information Management team, the Education and Outreach specialist, and university committees (Diving Safety, Small Boat Safety). Research direction, strategic planning, initiatives and policies are determined by consensus of an Executive Committee (the four Principal Investigators, plus three Associate Investigators who serve on a rotating basis). Policies regarding data access and sharing, use of MCR vehicles, boats and instrumentation, and collaborative activities with groups outside of the project are posted on our web site. We hold a 2-day MCR All-Investigator Meeting each year, attended by 40 to 50 MCR personnel, for a program of research presentations, training sessions, discussions and working group meetings.

SECTION 2 - PROPOSED RESEARCH

INTRODUCTION

The Moorea Coral Reef (MCR) LTER site, established in 2004, is an interdisciplinary, landscape-scale program whose goal is to advance understanding of key mechanisms that modulate ecosystem processes and community structure of coral reefs through integrated research, education and outreach. Our site is the coral reef complex that encircles the 60 km perimeter of Moorea (17°30'S: 149°50'W), French Polynesia (Fig. 1-1). Coral reefs are among the most diverse and productive of all ecosystems (Muscantine & Porter 1977, Hatcher 1990) and they have immense ecological, social and economic value (Moberg & Folke 1999, Brander et al. 2007). Increasingly, coral reefs are being affected by perturbations that range from short-term, localized disturbances - where return to the original state is possible - to more chronic, widespread influences of shifts in climate that may fundamentally alter the ecosystem (Connell 1997, Knowlton 2001, Gardner et al. 2003, Lesser 2007, Hoegh-Guldberg et al. 2007). Indeed, coral reefs are thought to be especially sensitive to changes in environmental drivers associated with climate, leading to the widely-held concern that climate forcing may cause dramatic changes in this ecosystem in the coming decades (Knowlton 2001, Lesser 2007, Hoegh-Guldberg et al. 2007). *A fundamental goal of the MCR is to advance understanding that enables accurate forecasts of the behavior of coral reef ecosystems to environmental forcing. To this end we seek to understand the mechanistic basis of change in coral reefs by: (i) elucidating major controls over reef dynamics, and (ii) determining how they are influenced by the major pulse disturbances and press drivers to which they are increasingly being subjected, especially those associated with global climate change (GCC)(Fig. 2-1).*

Coral reefs are among the most complex of biological phenomena and because of this complexity, we have an incomplete understanding of the abiotic forcing and biotic processes that collectively determine their structure and dynamics. Contemporary studies underscore the wide array of spatial and temporal scales necessary to attain an ecologically relevant understanding of their dynamics (Edmunds & Bruno 1996, Sebens et al. 1997, 1998, Murdock & Aronson 1999, Bellwood & Hughes 2001, Carpenter & Williams 2007, Schmitt & Holbrook 2007, Lenihan et al. 2008, Muller et al. 2009a, 2009b). They also emphasize the need to understand functional linkages across levels of biological organization - from molecules to the ecosystem. Hence, issues of scale and scale dependency connect much of our science program. Disentangling cause and effect relationships and forecasting responses of coral reef ecosystems require that we understand several types of scaling issues. For a start, most reef organisms have a bipartite life cycle and hence have demographically open, local subpopulations that are inter-connected via dispersal of early developmental stages. Many critical biological processes on the reef are influenced by the flow of water, and relevant hydrodynamic and oceanographic processes operate at spatial scales that range from the sub-millimeter to thousands of kilometers, and temporal scales that range from milliseconds to decades. It also is imperative to determine whether results found at one scale can be extrapolated to others. Synthesis and modeling can help resolve the general problem of, for example, predicting large-scale dynamics from small-scale processes (Chesson 1998) or scaling across levels of biological organization (Muller et al. 2009a, b).

Forecasting the behavior of an ecosystem to environmental forcing requires an adequate understanding of feedbacks across multiple ecological scales (e.g., Agrawal et al. 2007), including between structural and functional attributes (e.g., Cardinale et al. 2009). This level of knowledge does not yet exist for coral reefs, but the issue of feedbacks is particularly relevant because coral reef ecosystems are characterized by an exceptionally high prevalence of positive species interactions (Muscantine & Porter 1977). Indeed, the entire ecosystem depends on the well-known, but not sufficiently well-understood mutualism between scleractinian corals and their intracellular symbiont *Symbiodinium* (Apprill & Gates 2007). Facultative and obligatory mutualisms and

facilitations are common on tropical reefs (Stachowicz 2001), including several recently discovered by MCR investigators and students (Stewart et al. 2006, Bergsma 2009). Positive *indirect* interactions also are prevalent due in part to the nature and complexity of the food webs (e.g., Holbrook & Schmitt 2005, Holbrook et al. 2008a, Schmitt et al. 2009); theoretical and empirical work has shown the importance of such indirect interactions and feedbacks (Menge 1995, Bertness & Leonard 1997, Bruno et al. 2003, Thompson et al. 2006). Despite progress, positive interactions need to be incorporated more widely in ecological theory (Bertness & Callaway 1994, Bruno et al. 2003, Thompson et al. 2006). Even so, it will remain challenging to forecast responses to multiple stressors where positive interactions and positive feedbacks are pervasive.

A response of distinct interest to all LTER sites involves abrupt transitions from one community state to another with comparatively small changes in the value of a driver. Understanding the causes of such threshold responses and the nature of their reversibility are of great importance to ecology in general (Scheffer & Carpenter 2003) and coral reefs in particular (Hughes 1994). Many coral reef systems, particularly in the Caribbean, have undergone a rapid and persistent 'phase shift' (state change) from a coral to an algae dominated community (Gardner et al. 2003, Mumby 2009, Bruno et al. 2009). A variety of potential drivers of this shift have been forwarded, including loss of herbivores from disease and/or overfishing (Lessios et al. 1984, Hughes 1994), death of corals from disease (Bythell & Sheppard 1993), bleaching (Kramer et al. 2003) and/or physical disturbance (Bythell et al. 1993), and altered water quality (eutrophication) that favors algal growth (Littler et al. 1993, Hughes 1994). While some debate remains concerning these contributors (Aronson & Precht 2006, Burkepile & Hay 2006, Littler et al. 2006, Mumby & Steneck 2008), the issue of whether the state change represents a stable state maintained by positive feedbacks is not resolved (Mumby 2009). There is, however, evidence that a shift to algal domination may be reversible (Carpenter & Edmunds 2006, Idjadi et al. 2006, Mumby 2009). Further, the prevalence of coral – algal state change among geographical regions also is in question as a recent meta-analysis suggests that coral reefs in the Indo-Pacific may be comparatively resistant to blooms of macroalgae (Bruno et al. 2009), and that loss of living coral can lead to a 'coral depauperate' rather than 'algal dominated' state (Mumby 2009). Nonetheless, the balance between corals and algae on tropical reefs is likely to be affected in the future by global changes in seawater temperature and chemistry caused by elevated atmospheric $p\text{CO}_2$ (Hoegh-Guldberg et al. 2007).

Disturbance, a core theme of LTER sites, can have qualitatively different effects in a system with abrupt transitions depending on whether there exist positive feedbacks that result in alternative stable states. If there are, a disturbance of sufficient size alone can result in a shift between persistent states. In general there are two contrasting attributes of an ecosystem with respect to external drivers: 1) *resistance*¹, the amount of external forcing a system can absorb without a qualitative change and 2) *resilience*¹, the tendency of a system to return to its previous state after a perturbation. In this context, there are two attributes of resilience: the extent to which the system can be moved from its previous state and still return (amplitude), and if it does return, the speed with which it does so (elasticity). Resilience in particular will be one focus of MCR II because our site recently was subjected to a pulse disturbance that killed most living coral on the fore reef. The agent of disturbance was an outbreak of a predator, the crown-of-thorns seastar (COTS) *Acanthaster planci*, which appeared in large numbers in 2007 and peaked in abundance the following year (Fig. 1-2). In 2009, we received an NSF RAPID award to initiate a long-term field experiment to explore factors influencing the subsequent trajectory of the fore reef. The recent COTS outbreak is the latest of a

¹ Holling (1973) refers to resistance in this context as resilience; to avoid confusion, we use the definitions in theoretical ecology adopted from dynamical systems theory.

series of pulse disturbances that have affected the reefs of Moorea. In the past 30 years, they have been disturbed by cyclone-generated waves, bleaching from temperature excursions and a previous COTS outbreak (Adjeroud et al. 2009). While such pulse disturbances can kill coral tissue over large spatial scales, some (e.g., storm waves) also reduce three-dimensionality of the reef by pulverizing coral skeletons. While community structural attributes of coral reefs are influenced by reef architecture (e.g., Gladfelter et al. 1980, Carpenter & Williams 1993, Brooks et al. 2007, Schmitt & Holbrook 2007, Schmitt et al. 2009), resilience also may be affected by the extent of physical damage from a pulse perturbation (Connell et al. 1997).

Disturbances to the reefs of Moorea are occurring against a background of shifting environmental conditions arising from global climate change (GCC). Increasing atmospheric $p\text{CO}_2$ results in long-term press drivers to coral reef ecosystems via two pathways. The first is the well-known greenhouse effect that is warming the Earth. Global heating of the surface seawater is predicted to affect coral reefs both directly and indirectly. For example, the sensitivity of scleractinian corals and their endosymbionts (*Symbiodinium*) to increasing seawater temperature is well known (e.g., Hoegh-Guldberg 1999), and warming seawater also can alter the frequency and intensity of such important pulse disturbances as cyclonic storms (Emanuel 2005). The second pathway arises from changes in ocean chemistry due to rising concentrations of CO_2 in seawater, termed ocean acidification (OA) (Doney et al. 2009). This increased carbonization of the ocean is likely to influence directly key ecosystem processes of coral reefs, including rates of calcification, C-fixation by photosynthetic organisms, and N-fixation by cyanobacteria (Doney et al. 2009). Because of the fundamental importance of calcifying organisms, much of the work to date on effects of ocean acidification on tropical reefs has focused on calcification (e.g., Hoegh-Guldberg et al. 2007), and it is revealing complex interactions between OA and temperature (e.g., Reynaud et al. 2003) or nutrients (e.g., Langdon & Atkinson 2005). For example, increased concentrations of CO_2 in seawater acted synergistically with temperature to lower the thermal bleaching threshold of coral (Anthony et al. 2008). Thus, not only is there potential for OA alone to produce antagonistic or interactive responses by affecting a number of important rate processes, it also can result in complex, non-linear responses in combination with other external pulse or press drivers.

CONCEPTUAL FRAMEWORK, ORGANIZING THEMES & KEY DRIVERS

General Conceptual Framework. A central goal of the LTER Network is to understand how external drivers that operate over different temporal and spatial scales interact to influence community structure and ecosystem processes. The 2007 LTER decadal plan (www.lternet.edu/decadalplan/) presented a conceptual framework to (i) facilitate network-level and cross-site research and (ii) provide an integrated approach to address social-ecological questions. The ecological and social dimensions of the Integrated Science for Society and Environment (ISSE) framework are connected at one end by external press and pulse drivers of ecological change that are influenced by human behavior, and at the other by services provided by ecosystem; five generic questions form an iterative chain of information pathways that link the components (U.S. LTER 2007). For MCR II, we adopt and 'operationalize' the relevant ecological and geophysical portions of the ISSE framework (Fig. 2-1), which positions us to add social dimension and ecosystem services linkages as appropriate funding opportunities arise. In the context of our renewal, the two relevant ISSE questions are: Q1: *How do long-term press disturbances and short-term pulse disturbances interact to alter ecosystem structure and function*; and Q2: *How can biotic structure be both a cause and consequence of ecological fluxes of energy and matter*? The ISSE framework is an appropriate construct around which to organize MCR II research, to foster cross-site comparisons, and to position us for future participation in ISSE activities.

Organizing Themes. The central issue that motivates the research is to understand how external drivers, especially those associated with global climate change, interact to influence the structure and function of coral reefs. Our proposed research is organized around the following three themes that connect to our framework (Fig. 2-1; Table 2-1):

- (1) INTERACTIVE EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION**
- (2) INDIRECT EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION**
- (3) EFFECTS OF STRUCTURE - FUNCTION FEEDBACKS ON RESISTANCE AND RESILIENCE**

“Pulse” and “press” as used above are perhaps best viewed in terms of the duration of a perturbation relative to the response time of the dependent variable of interest. Ocean temperature, for example, can be both a press driver (e.g., the nearly monotonic rise in mean annual ocean temperature over the past several decades) and a pulse disturbance (e.g., brief temperature excursions that can trigger bleaching). Of course, short-term (seconds to months) external drivers that affect reefs are embedded within a climatic regime that varies over much longer time scales (years to decades), and we recognize that pulse and press drivers can have both direct and interactive effects on the structure and function of the ecosystem (Theme 1, Fig. 2-1). Further, like all ecosystems, the structure and processes of a coral reef community are linked such that a driver that affects structure (e.g., species composition) can indirectly alter the rate of ecosystem processes (e.g., reef metabolism) (Theme 2; Fig. 2-1). Important positive and negative feedbacks between structure and function almost certainly arise from these indirect effects (Theme 3; Fig. 2-1). The extent to which coral reefs can absorb perturbation without qualitative change, or return to the pre-disturbance condition if altered, often depends on the nature of these feedbacks, the biology of the organisms and the interactions among the major players (Theme 3; Fig. 2-1).

Major Press Drivers. During MCR I, we began to identify the major press and pulse drivers of community structure and ecosystem function. Although we anticipate that additional important drivers will emerge in the future, we now recognize the events that are most likely to affect the reefs over the coming decades. Interestingly, the last five years has seen a virtual paradigm shift in evaluating the importance of selected press stressors on coral reefs. In the relatively recent past, the focus was almost entirely on rising temperature from global warming as a major climatic driver of coral mortality (Hoegh-Guldberg 1999). It now appears likely that the press driver that may ultimately cause the greatest ecological change to tropical reefs is ocean acidification (OA) (Hoegh-Guldberg et al. 2007). It is conceivable that scleractinian corals will cease to exist as a calcified taxon within this century as atmospheric CO₂ surges past the current level of 380 ppm (Veron et al. 2009); for corals that might endure this challenge, rising seawater temperature brings the risk of bleaching (Hoegh-Guldberg & Salvat 1995). Additionally, rising sea level will alter important hydrodynamic conditions like circulation patterns and cross-reef transport (e.g., Hench et al. 2008). These large spatial scale phenomena associated with global climate change occur against a backdrop of additional press drivers that arise from local human activities such as fishing, which alone can result in dramatic alteration in structure and function of coral reefs (Roberts 1995, McClanahan et al. 1999). Overfishing has long been considered a major threat to coral reef ecosystems (Roberts 1995), and it can interact with other stressors to impair both the resistance and resilience (e.g., Hughes 1994). The two primary press drivers we will focus on for MCR II are changes in ocean carbonization associated with OA and rising seawater temperature associated with global warming. Rising sea level and increasing fishing pressure will be considered to a lesser degree.

Major Pulse Drivers. The history of disturbances to the reefs of Moorea reveals that three types of pulse perturbations have each occurred at least twice during the past 30 years. Since 1980, the reefs have been disturbed by two powerful cyclones (1982, 1991), four bleaching events of varying magnitude (1991, 1994, 2002, 2003) and two

COTS outbreaks (1991, 2008) (Adjeroud et al. 2009). Additionally, waves damaging to reefs have been generated as far away as the Antarctic Southern Ocean to the southwest and the Bering Sea to the north. Hence, decadal-scale climate phenomena such as the Pacific Decadal Oscillation (PDO) in the northern hemisphere and the Antarctic Oscillation [AAO; also called the Southern Annular Mode (SAM)] can influence Moorea through the propagation of wave energy. There are at least two ways that wave disturbance can be influenced by press drivers associated with GCC; rising sea levels may increase the risk of wave damage to corals in lagoons by reducing the moderating effect of the offshore barrier on wave energy (Symonds et al. 1995), while rising sea surface temperature has the potential for increasing the frequency and intensity of large storms (Emanuel 2005). The most common cause of regional-scale bleaching of coral (i.e., loss of *Symbiodinium*) is thermal stress caused by high water temperature over just a few weeks (Hoegh-Guldberg 1999). There appear to be important interactions between temperature fluxes and other stressors that increase the potential for bleaching, including solar radiation (Gleason & Wellington 1993) and OA (Anthony et al. 2008). Important biotic pulse disturbances include outbreaks of coral predators, principally COTS, and of coral disease. While the reefs of Moorea have just experienced the second of two COTS outbreaks in the past thirty years, the corals have not been subjected to a major disease epidemic during that period. However, rising seawater temperature associated with climate warming can increase the potential for disease epidemics by, for example, increasing the population growth rates of coral pathogens (Harvell et al. 2002, Bruno et al. 2007). Furthermore, there is growing evidence that the relationship between temperature, coral disease and bleaching is complex; bleaching can lower resistance of corals to disease and, in turn, coral disease can reduce the resilience of a coral following bleaching (Brandt & McManus 2009).

SITE DESCRIPTION

Moorea is located in the central south Pacific 20 km west of Tahiti, 4,400 km south of Honolulu and 6,600 km southwest of Los Angeles (Fig. 1-1). It is a triangular volcanic 'high' island with an offshore barrier reef that encloses a system of shallow (mean depth ~ 7 m), narrow (~ 1 - 1.5 km wide) lagoons around the 60 km perimeter of the island (Fig. 1-1). The MCR site encompasses the area around the island bounded inshore by land and, except for certain oceanographic measurements, offshore by the 20 m depth isocline on the fore reef slope (Fig. 1-1). It contains the three major coral reef habitat types (fringing reef, back reef, and fore reef) and twin bays on the north shore (Fig. 1-1). The fore reef slopes rapidly to several hundred meters, and stony coral can grow as deep as 40 m. Internal waves occasionally impinge on the fore reef and may be a source of new nutrients to the reef system. Moving shoreward from the reef crest, domination of the bottom by 'pavement' and comparatively small coral 'bommies' (patch reefs formed by coral) on the back reef grades into rubble and sandy areas with much larger bommies that eventually give way to dominance by fine sand closer to shore. Coral grows up to the shoreline to form a fringing reef (Fig. 1-1). Twin deep bays formed by two rivers bisect the north shore, and are a source for terrigenous organic and inorganic materials to the reef. These and smaller watersheds have produced three to five passes in the barrier reef on each side of Moorea (Fig. 1-1). Ocean waters enter lagoons over the reef crest and exit through the passes. Offshore wave climate is a major driver of current speeds within the lagoon. Swell prevails from the southwest in the Austral winter and from the north in the summer, resulting in seasonality in exposure of different sides of Moorea to large waves and high flows. Moorea lies near an amphidromic point, and tidal amplitudes are small (~ 30 cm maximum).

GENERAL APPROACHES

Evaluating the interactive effects of press and pulse drivers on the coral reefs of Moorea not only dictates a long-term research program, it requires a multi-pronged approach. Certain drivers of coral reef ecosystems are amenable to *in situ* manipulation (e.g.,

physical disturbance that pulverizes coral skeletons), while it is impractical or impossible to manipulate others in the ocean in a meaningful way (e.g., seawater temperature). Because of this, our proposed research will use a variety of approaches that include: (1) spatially-explicit time series measurements of key external drivers and ecological response variables; (2) long- and short-term field and mesocosm experiments to isolate causal mechanisms underlying observed patterns and/or explore potential synergies, (3) integrated process studies to gain mechanistic understanding of processes that cannot otherwise be addressed and to help scale up results of field and mesocosm experiments; and (4) integration and modeling to facilitate predictions beyond the spatial and temporal scope of MCR data and help guide future research.

Spatially-Explicit Time Series Measurements. The MCR Time Series Program (Table 2-2) has been designed specifically to: (i) measure spatially-explicit temporal patterns in the structure and function of the coral reefs of Moorea, together with the physical and chemical forcing variables that influence them, (ii) provide a contextual basis for our process-oriented studies, (iii) provide parameter estimates for modeling efforts, and (iv) meet the needs for comparative analyses within the LTER network, including those related to the five core areas of LTER research². Our time series framework stresses the integration of repeated abiotic and biotic measurements made across several spatial scales. While the detailed nature of time series information is driven by our site science and anticipated long-term changes, it also enables cross-site comparisons.

Field and Mesocosm Experiments. During MCR I, the site experienced a large pulse disturbance in the form of an outbreak of COTS that killed most living coral on the fore reef (Fig. 1-2). Such a disturbance, unique to Indo-Pacific coral reefs, provided us with an unparalleled opportunity to explore experimentally factors that directly, indirectly and interactively influence reef resilience, structure and function. We received an NSF RAPID grant in 2009 to initiate a long-term field experiment, described below, to mimic disturbances that kill coral tissue but either leave or remove coral structure; these pulse disturbances are crossed with a press manipulation that mimics light or heavy fishing pressure to explore interactive effects. Shorter-term manipulations will be nested within the long-term experiment to further explore specific features underlying the response of various structural and functional attributes of coral reefs. Because some important external drivers are difficult or impossible to manipulate meaningfully in the field, we have constructed a state-of-the-art OA mesocosm facility at the Gump Station with NSF supplemental funds. It currently consists of 12 tanks in which light, temperature and $p\text{CO}_2$ can be controlled to test hypotheses regarding the individual and synergistic effects of major global climate change drivers. The system uses gas mixing technology to manipulate $p\text{CO}_2$ and create step-less adjustment within a range simulating atmospheric conditions expected under climate projections. It is scalable, supports experimental volumes from 2 – 200 liters, and can be used for both tanks and flumes.

Integrated Measurement-based Process Studies. Experiments are neither always practical nor necessarily appropriate for unraveling details of important processes or the causes of the patterns they produce. We will undertake field campaigns that involve intensive, coordinated sampling to help reveal the mechanistic underpinnings of such important processes as reef metabolism, nutrient flux, and carbon cycling (Fig. 2-2). With caution, such studies can provide insight into potential effects of climate forcing by the judicious substitution of space for time, and also help to scale up results of field and lab experiments. Additional studies will focus on patterns and dynamics of diversity of *Symbiodinium* in corals (Fig. 2-3).

² (i) dynamics and control of primary production; (ii) population dynamics of representative groups; (iii) pattern and control of organic recycling; (iv) pattern of inorganic input and nutrient dynamics; (v) patterns and consequences of disturbances that arise from or induce long-term trends

Integration and Modeling. Integration of MCR observations and experimental results will be achieved using a suite of analyses and models, including quantitative (e.g., DEB and ODE-based models) as well as qualitative and statistical constructs (e.g., food web path models, structural equation modeling). We will use a systems biology framework to both integrate disparate observations and scale across levels of biological organization that range from sub-organismal (e.g., DEB model specifying flows of matter and energy among host coral, *Symbiodinium* and environment; Fig. 1-5) to the ecosystem [e.g., integrated physical (e.g., circulation) and biological (e.g., genetic) models of reef connectivity via transport of materials]. Modeling allows informed predictions of physical and biological processes that extend beyond the spatial and temporal scope of our data, and helps identify promising avenues for future research.

TIME SERIES PROGRAM AND LONG-TERM EXPERIMENT

A significant amount of MCR II science resources will be devoted to the time series program, maintaining a newly-established long-term field experiment to explore resilience, and managing the resultant data from these and our other science components. Table 2-2 summarizes the time series program, and relevant datasets. The long-term experiment will address several of our major research questions, and will be a platform for shorter-term manipulations to address specific factors influencing reef structure and/or function.

Time Series Program: Our time series program has a spatially stratified, hierarchical sampling design. Depending on the taxon or process, the scale and scope of the measurements encompass a variable number of sites, habitat types, depths, or frequencies of sampling (Table 2-2). The most spatially inclusive sampling includes three habitat types [fore reef (10 m and 17 m depth), back reef, fringing reef] at two localities on each of the three shores of Moorea (Fig. 1-1). Biotic factors surveyed within quadrats or along fixed transects include aspects of ecosystem function (e.g., primary productivity), community-level attributes (e.g., trophic structure, diversity), population-level characteristics (e.g., abundance, dynamics), and individual-based characteristics (e.g., demography, functional metrics). In addition to collecting standard surface climate data, other oceanographic abiotic factors that affect reef organisms are sampled repeatedly through time (Fig. 2-4). We have established one heavily-instrumented site and one less-instrumented site on each of Moorea's three shores. These deployments Fig. 1-1) are < 25 m from the fixed transects where biotic surveys are conducted. Regional scale properties (e.g., sea-surface temperature, sub-surface chl *a* concentration, regional surface currents) are estimated via remote sensing using existing satellite sensors (Fig. 2-4).

Physical and Chemical Measurements. Coral reefs are physically-forced systems, and we have instrumented the reefs with multiple sensors to measure factors known to influence coral reefs: temperature, light (including UV), nutrient availability, and water flow (which primarily is wave-driven). In addition, salinity, turbidity, inorganic nutrients, aspects of seawater chemistry and the hydrographic structure and variability associated with the water column seaward of the reef sites are measured. We will continue measuring pH periodically in our offshore sampling station as part of our routine hydrographic time series sampling, but will begin more frequent measurements of pH and total alkalinity (TA) to begin to understand patterns and causes of variation in total alkalinity of seawater bathing the reefs. Measurement of seawater temperature using high resolution thermistors (± 0.01 °C resolution) will be made every 2 minutes in three habitats (fore reef 10 m and 20 m; back reef) at all sites. Seawater temperature on the fringing reefs at all sites will be measured with lower resolution (± 0.2 °C) thermistors at two depths (1 m and 5 m). On the fore reef at LTER sites 1, 4 and 5, additional high resolution thermistors will continue to be deployed on vertical mooring lines at 5 depths (7, 9, 11, 15 and 17 m) and CTD (Conductivity, Temperature, Depth) recorders will be

deployed at two depths (5 m and 13 m). Additional instrument arrays on the fore reef of these three primary sites will include sensors to characterize tidal height, current speed and direction and offshore wave climate (height, direction, periodicity); simultaneous measurements of wave heights and currents are critical given that water flow in lagoons and local circulation patterns are driven primarily by the offshore wave climate (Figs. 1-6 – 1-8). Measurements of photosynthetically active radiation (PAR) levels will be taken continuously at our met station and periodically on the reef (LTER 1) concomitant with measurements of reef metabolism. We will expand surface PAR sampling to the east (LTER 4) and west (LTER 5) shores, and currently are testing instruments that will support long-term underwater PAR measurements. Water column hydrographic profiling and estimates of organic and inorganic nutrient concentrations will be done twice annually at the fringing reef, lagoon and fore reef habitats at one site (LTER 1), a site 5 km offshore, and at several sites within Cook's Bay. Except for the offshore station, regular nutrient sampling will be augmented by additional samples of organic and inorganic nutrients collected from these same locations periodically throughout the year. Oceanographic instrumentation will be complemented by surface environmental data from our met station (solar irradiance, atmospheric pressure, wind speed and direction, air temperature, relative humidity and rainfall) deployed at the Gump Station, and by additional meteorological stations operated by Météo France at locations on all three shores of the island (Fig. 2-4). Larger-scale observations of current and water mass variability come from satellite remote sensing of currents (TOPEX Poseidon, ERS, altimeter satellites), temperature (AVHRR), and ocean color (SeaWiFS, MODIS) (Figs. 1-8 & 2-4; Maritorena & Siegel 2005, Maritorena et al. 2002, 2009, Reynolds 1988, Reynolds & Marsico 1993.). Data on deep, ocean swell impinging on Moorea and synoptic scale meteorological variability will continue to be obtained from ongoing monitoring programs in French Polynesia. Data from satellite sensors are used to measure spatial and temporal variation in sub-surface concentration of chl *a*, light absorption caused by dissolved and detrital matter, particulate backscattering and Sea-Surface Temperature (SST) at the Moorea and regional scales.

Community Structure and Ecosystem Function Measurements. Reef metabolism, including primary production and respiration, will be estimated annually on the north shore using a control volume approach. Vertical profiles of water column primary production also will be measured annually using standard ^{14}C tracer/bottle techniques offshore, inshore and on the back reef at LTER 1. Nutrient (NO_2^- , NO_3^- , PO_4^{3-} , SiO_4^{2-}) concentrations will be estimated concomitantly with measurements of water column primary productivity, as will bacterioplankton biomass, production as well as DOC and DON concentrations. Estimates of bacterioplankton biomass and production rates will include coral interstices. DOM re-mineralization experiments (Carlson et al. 2002, 2009) will assess the available organic matter and growth efficiencies of the heterotrophic prokaryotes at offshore, above reef and reef interstitial sites.

We will continue to quantify, to the lowest taxonomic resolution possible (typically species or genus), the abundances of various types of benthic algae, scleractinians, other macro-invertebrates, and fishes at the 18 permanent habitat / site combinations (i.e., fringe, back reef, fore reef at LTER sites 1 – 6). Abundances are estimated yearly either visually or photographically (corals). Abundance and sizes of coral-associated fishes will be assessed along permanent transects. The numbers of herbivorous echinoids and gastropods and of corallivorous echinoderms are counted in 1 m^2 quadrats at randomly selected but temporally fixed locations along each transect. Scleractinian corals, macroalgae, crustose coralline algae, algal turf, and bare space will be photographed digitally in these quadrats and analyzed for percentage cover. In addition, we will sample annually the physical attributes and associated fishes of 66 large, permanently marked *Porites rus* colonies in the lagoon, a legacy time series component that was initiated in 2000. Based on analyses of data and assessment of

our needs, measurement of zooplankton abundance, biomass (dry weight, organic carbon), and composition will be discontinued as a regular feature of the time series program (during MCR I, these had been assessed at LTER 1, the 5 km offshore station and at several sites within Cook's Bay two or three times per year); zooplankton samples will be gathered during relevant process-oriented studies.

We will continue to estimate coral settlement and recruitment at our north shore sites (LTER 1 and 2 at 10 m and 17 m depths) and at several lagoon locations using settlement tiles deployed for 6 month periods. To estimate inter-annual variability in settlement of lagoon fishes, we will continue daily quantification of settlement of planktivorous fish to Gump Reef from mid-June through August, which we have done annually since the early 1990's (Fig. 2-5).

Long-Term Experiment: Understanding resilience can be especially challenging when ecosystems experience multiple perturbations that, in combination, can cause complex, non-linear community dynamics. The recent COTS outbreak provided an opportunity to address several key questions regarding resilience, including the trajectory of the system following disturbances that affected different components of the ecosystem, and the existence and strength of positive feedbacks that might produce alternate persistent states. The COTS outbreak killed almost all coral on the fore reef (Fig. 1-2), allowing us to perform a manipulation (removal of dead coral skeletons) to mimic two qualitatively different disturbances: those that kill coral but leave their skeletal structures intact (e.g., COTS, disease, bleaching) and those that also reduce reef dimensionality by pulverizing coral skeletons (e.g., storm waves). Additional treatments can be nested within or crossed with this basic, long-term manipulation to explore how other factors interact with these qualitatively different types of disturbance, and to focus on such components as the microbial and *Symbiodinium* consortia. We will maintain a set of additional treatments (i.e., fish exclusion cages, cage controls, controls) to explore possible interactions of these pulse disturbances with overfishing, a press driver.

We initiated the experiment following the collapse of the most recent COTS outbreak (August 2009). Twenty permanent 5 x 5 m plots were established at 12 m depth on the fore reef near LTER 2. After plots were permanently marked but before any manipulation was performed, plots were photographed (0.25m² quadrats). Nearby plots were paired and divers removed all dead coral structure from one randomly selected member of the pair to simulate physical disturbances that reduce structural heterogeneity. Manipulated plots were immediately re-photographed. Abundance and percent cover of corals, coralline and foliose algae will be estimated from digital photographs taken annually during MCR II and beyond. Surveys of fishes and (non-coral) macro-invertebrates were made on each plot before and just after the dead structure was removed; these also will be continued annually. Seawater samples from the water column, just above the substrate and from the interstitial spaces within each plot will enable characterization of the microbial community (Fig. 2-2) present at the initiation of the experiment; the microbial community will be sampled annually. Sets of settlement tiles were placed within each plot to quantify colonization by coral, other sessile invertebrates and algae. Tiles will be sampled once (algae, sessile invertebrates) or twice (coral) annually.

RESEARCH QUESTIONS AND PROGRAM

A list of the research questions, projects and associated MCR personnel is provided in Table 2-1. Figure 2-1 shows how our themes and questions relate to our conceptual framework, and integration of our research components is shown in Figure 3-1. Below we give the rationale and approach for addressing each question.

THEME 1: INTERACTIVE EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION

The dynamics of reefs are driven by multiple pulse disturbances that operate in concert with press drivers acting on decadal or longer time scales. As noted above, rising

seawater temperature from increasing atmospheric CO₂ and changing seawater chemistry from coupled increases in pCO₂ in the ocean define the most important suite of press disturbances affecting coral reefs in the 21st century; pulse disturbances are superimposed upon these climate drivers. Although a large literature addresses thermal aspects of global climate forcing for corals (Jokiel 2004), studies of OA are still in their infancy (Fabricius 2008, Vezina & Hoegh-Guldberg 2008), and virtually nothing is known of their interactive effects on corals and other coral reef organisms.

Question 1A. What is the nature of the functional responses by foundation taxa to major Global Climate Change drivers?

Rationale: Following the first large-scale coral bleaching episodes in the 1980's, links were quickly forged with the thermal signature of Global Climate Change (GCC) (Hoegh-Guldberg 1999). More recently, however, OA emerged as the "other CO₂ problem" (Doney et al. 2009) in recognition of the dual role of CO₂ in global warming, and in seawater to reduce pH, depress aragonite saturation state (Ω_a), impair biogenic calcification and alter other important ecosystem rate processes (Hoegh-Guldberg et al. 2007, Doney et al. 2009). The current condition and future trajectories of reefs are the combined result of press and pulse disturbances acting over local, landscape, and regional scales. The state of reefs on small scales is, therefore, likely to be affected by local processes, but the mode of action of these phenomena will be dependent upon the regional bio-physical context. Describing these relationships will be challenging as the mechanisms underlying biological processes typically are non-linear functions of physical conditions, often as a result of enzyme kinetics (Somero 2004), and characterized by a threshold response flanked by zones of rapid changes.

Approaches: Question 1A primarily will be addressed with mesocosm experiments to measure the response of corals and coralline algae to the individual effects of GCC drivers. *First*, we will explore these effects to (i) test the hypothesis that taxa are not affected equally by GCC and (ii) estimate the (non-linear) relationships between GCC drivers and metabolism (photosynthesis and calcification). This initiative builds on the foundational studies of the effects of GCC on corals and coralline algae (Hoegh-Guldberg 1999, Langdon 2000, Jokiel 2004, Kleypas & Langdon 2006) by broadening the taxonomic breadth of study organisms, expanding the range of treatment levels, and tightening the control over the recent history of the organisms. As a rationale, we note that < 20 coral species have been studied for the effects of OA (Kleypas & Langdon 2006), most studies of temperature on corals and algae utilize only 2-3 treatments (Jokiel 2004), and growing evidence highlights the importance of history (i.e., acclimatization) in the responses of corals (Middlebrook et al. 2008). We will use our new mesocosm facility to create OA and temperature treatments. To estimate non-linearity, multiple treatments for temperature (\approx 24, 26, 28, 30, 32°C) and for OA (380 [present], 600, 800, 1000, 1200 μ atm CO₂) will be established, and the responses assessed at the organismic level for multiple species of corals and algae. Response variables will be photosynthesis and calcification, as both processes play critical roles in community function, and are functionally linked in corals (Allemand et al. 2004) and algae (Nelson 2009). An important component will be evaluating rates of dissolution of carbonate sediments as a function of OA. There is evidence that OA will affect both rates of calcification (Langdon et al. 2000) and dissolution (Yates & Halley 2006, Andersson et al. 2007), and the balance between these processes will determine net accretion. These experiments will measure the dissolution kinetics of corals and reef cements under different OA conditions, initially focusing on high Mg-Calcite containing organisms (e.g., CCA), then corals (that form aragonite), and finally, possible interactive effects (Question 1B). *Second*, to explore underlying causes, we will apply molecular tools to identify the genes being expressed as a result of exposure to GCC drivers. The application of these tools to an echinoderm system has identified genes responsible for regulating calcification under OA conditions (O'Donnell et al. in press). We expect that

such tools will identify normal and novel pathways of responses to GCC. Such pathways likely will include acclimatization to both temperature and OA (Edmunds & Gates 2008), although it is unknown whether such capacity can ameliorate the impacts of GCC. To explore this, we will investigate the physiological and molecular basis of acclimatization in corals to temperature and OA, as well as test the Beneficial Acclimatization Hypothesis that posits acclimatization enhances fitness (Huey et al. 1999). This is motivated by the potential for mapping the capacity for plasticity by corals to GCC, and for identifying genotypes with the capacity to resist GCC. For symbiotic corals, this capacity is rich as the shuffling of *Symbiodinium* (Baker et al. 2008) has the potential to create a “new” holobiont. *Third*, we recognize the complexity of the biological responses we propose to address, and are cognizant of the limitations of linear and additive constructs for synthesizing our data. To address these problems, we have been developing a Dynamic Energy Budget model for symbiotic mixotrophs (Muller et al. 2009a, b; Fig. 1-5), and are currently refining the model to integrate the effects of GCC on the performance of corals, algae, and coral reefs (see Integration and Modeling). We aim to use our DEB models as a tool in an experimental context, and to enhance our capacity to project future coral community structure.

Question 1B. What are the synergistic effects involving Ocean Acidification and seawater temperature on key metabolic processes?

Rationale: Understanding effects of GCC on corals, coralline algae, and coral reefs begins with an analysis of each driver in isolation (Question 1A), but relevancy requires an analysis of interactive effects. One striking example is the synergistic effect of temperature and OA on coral calcification (Reynaud et al. 2003, Anthony et al. 2008). It is likely that similar interactions characterize the effects of GCC on other key processes such as photosynthesis, carbonate dissolution, N-cycling and C-cycling. Further, the interactive effects between temperature and OA can be complicated by such other factors as nutrients (Atkinson & Cuet 2008, Cohen & Holcomb 2009), flow speeds (Patterson 1992), and light intensity. Here we build on the univariate analyses (Q 1A) through lab experiments designed to explore interactive effects of key GCC drivers.

Approaches: *First*, we will expand the analyses of the effects of GCC on the calcification of corals and coralline algae by addressing interactive effects involving alkalinity, temperature, water flow, and nutrients. We will conduct experiments in which factorial combinations of Ω_a and temperature, nutrients, or flow will be created, and the responses assessed will be rates of calcification and photosynthesis. These experiments also will be completed with combinations of taxa (i.e., artificial communities) in mesocosms, and with *in situ* studies exploiting locations in Moorea where temperature and Ω_a vary naturally. [While beyond the scope of this proposal, these efforts help us build toward implementation of a Free Ocean Carbon Experiment (FOCE) (Kirkwood et al. 2007) in Moorea.] We also will scale up analyses of carbonate dissolution to address the interactive effects of Ω_a , temperature, nutrients, and microbial metabolism on the dissolution of reef carbonates. *Second*, research within our group and collaborators (Knowlton & Rohwer 2003; Fig. 2-2) is beginning to identify the diverse roles fulfilled by the microbial consortia associated with corals, and we will start to address the impacts of GCC on microbial consortia. Informed by the spatial analyses of microbial consortia and DOM across the reef (Fig. 2-2), we will explore the diversity and functional biology of bacteria associated with interstices of coral colonies and the coral surface microlayer (CSM), and test for interactive effects of Ω_a and temperature on microbially-mediated C-cycling. These analyses will take place in the field and mesocosms with the objective of developing the capacity to scale among functional levels. As microbial communities play critical roles in N-recycling on tropical reefs (Alongi et al. 2006), our analyses of interactive effects of GCC drivers will explore impacts on N-recycling by linking with our studies of N-fixation using acetylene reduction techniques (Larkum et al. 1988).

Question 1C. How do pulse drivers interact with a key press driver (fishing) to influence community structure?

Rationale: Interactions between pulse and press drivers likely have substantial effects on coral reef community structure. In Moorea, the response of reefs to the recent COTS outbreak (a pulse event) is superimposed on long-term (press) effects of temperature, OA and human activities (e.g., fishing). Thus, while COTS outbreaks have occurred in the Pacific since at least the 1960's (Moran 1986), the response of contemporary reefs to COTS may differ from that recorded previously because of changed physical environments and differing biotic contexts (e.g., fishing, altered relative abundance of foundation taxa). The effects of COTS likely cascade through the reef community, potentially by altering coral recruitment, vacant space (Moran 1986), three-dimensional structure that serves as habitat for fishes, invertebrates and algae (Holbrook et al. 2002a, 2002b, 2008b), and modifying the chemical micro-environment adjacent to the benthos where microbial communities are functionally diverse (Hewson & Furhman 2006). Dimensionality of the reef can be reduced by physical disturbances (e.g., large storms), and this architectural attribute can influence the rates of biotic interactions such as predation, corallivory, and herbivory (Holbrook & Schmitt 2002, Lenihan et al. submitted). Heavy fishing potentially can influence the state of the community by, for example, affecting the ability of herbivorous fish to control algae (Hughes 1994). Hence, the joint influence of fishing and a pulse event may differ depending on whether the disturbance alters reef architecture. For MCR II, we will test the following hypotheses: (i) overfishing increases the probability of a shift to an algae dominated state following a pulse disturbance because of reduced abundance and size of herbivorous fishes; and (ii) in the absence of overfishing, pulse disturbances that leave coral skeletons intact are more likely to lead to an algae dominated state because structural heterogeneity reduces the efficacy of herbivory.

Approaches: Our long-term field experiment, described above, will be the primary platform to address the interaction of fishing and different types of pulse disturbances. To simulate overfishing, wire mesh cages (0.75m² in area) and made of hardware cloth (mesh = 2.5 cm) were placed over three randomly chosen sets of coral settlement tiles within each of the twenty 5 x 5 m plots. Cages are intended to exclude medium to large-bodied fishes, including herbivores and corallivores that are relatively abundant on Moorea (sea urchins are uncommon on the fore reef). Half cages were placed over an additional three sets of randomly selected tiles within each plot to control for possible artifacts (e.g., altered light level, water velocities) associated with the cage structure. The remaining three sets of settlement tiles within each plot were left exposed. Five additional high-resolution digital images of haphazardly chosen 0.01 m² quadrats around each set of tiles were recorded; photographs will be taken annually to document coral recruitment to the natural reef substrate.

THEME 2: INDIRECT EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION

The research proposed in this section focuses on how specific press and pulse drivers can affect community structure and/or ecosystem function *indirectly* by altering processes that change either structure or function. We define 'community structure' broadly as encompassing, among others, the population dynamics of key species, trophic composition of the reef community, the relative abundance of species (including community state), and species diversity. Ecosystem function is defined broadly to include such important ecological processes as reef metabolism, secondary production, nitrogen fixation and nutrient cycling, and the provision of habitat.

Question 2A: How do changes in structure affect ecosystem function?

Rationale: The relative abundances of coral species are controlled by a suite of factors and interactions that often results in the disproportionate mortality of coral functional forms and shifts in the relative abundances of corals and other benthic organisms. For example, coral bleaching, COTS, and wave energy often reduce the abundances of

branching corals (e.g., acroporids, pocilloporids), thereby increasing the relative abundance of more massive corals (e.g., poritids) (Loya et al. 2001) and opening space for colonization by algae. This change can have dramatic effects on other aspects of the community as branching corals exhibit high rates of primary production and calcification, and provide habitat for a diversity of coral-sheltering fishes (Brooks et al. 2007, Holbrook et al. 2002a, 2002b, 2008b). Additionally, colonization and community development on the dead coral skeletons can shift community composition toward algal domination (Mumby 2009) and the degree to which this occurs will depend on the abundance and diversity of herbivores and corallivores that affect recruitment and survivorship of macroalgae and corals (Burkepile & Hay 2008, Mumby 2009, Sotka & Hay 2009). Several of these processes likely vary across the strong gradients in water flow that exist over multiple spatial scales on Moorea reefs (Hench et al. 2008) and more subtle effects of flow-induced changes in coral morphology and reef spatial heterogeneity on structure/function may also be important.

Approaches: *First*, we will continue to explore the relationships between aspects of the flow environment (means/variances in velocity, turbulence) and the structure of the benthos over a range of spatial scales by focusing on organisms and sections of reefs that vary in morphology, spatial heterogeneity and community structure. These investigations will focus on how physical structure and species composition modify local hydrodynamics and how this might affect community development and maintenance. *Second*, we will exploit gradients in flow across the reef to test hypotheses about how variation in coral colony morphology interacts with flow to provide suitable habitat for coral-sheltering fishes and invertebrates, and how this may affect the microbial community associated with corals and their interstitial spaces. Since habitat suitability determines the abundances of sheltering fishes, which influences the local nutrient environment, effects on coral growth (Holbrook et al. 2008a; Fig. 1-13) and the microbial community structure and function are likely. *Third*, we will explore how the composition and diversity of communities associated with corals could change with shifts in the relative abundance of coral morphotypes. We will do this first by using survey data to compile likely assemblage structures for communities composed of differing relative abundances of common coral microhabitats (that simulate scenarios of change). We will test these predictions by assembling small patch reefs (~2 m dia) on sandy bottoms.

Question 2B: How do changes in function affect community structure?

Rationale: Like most benthic marine systems, water motion in coral reef ecosystems not only can be a pulse disturbance (via wave energy), it plays a fundamental role in the fluxes of key materials to the reef. Factors that affect this connectivity therefore can have substantial indirect effects on the structure of the community. We are documenting long-term patterns of regional connectivity (e.g., Bernardi et al. 2003), transport of seawater across the reef crest into the lagoon (Hench et al. 2008) and counter-clockwise around the island (Fig. 2-7), as well as physical forcing of the delivery of larvae (fish and coral; Schmitt & Holbrook 2002a, 2002b, Bernardi et al. in prep., Edmunds et al. in prep.) and the flux of zooplankton (Alldredge & King 2009). Rates of primary production and nutrient uptake also are linked closely to hydrodynamics through mass transfer-related dynamics (Falter et al. 2006, Carpenter & Williams 2007). Changes in flow over the reef as a result, for example, of predicted sea-level rise would be expected to affect rates of reef primary production and perhaps calcification. Whether the drivers are pulse or press, the resulting alterations in ecosystem function may have significant effects on community structure. For example, these changes might be manifest in altered population dynamics of key species and/or changes in growth rates and competitive interactions that alter the relative abundances of species. This could result in changes in diversity and altered trophic relationships.

Approaches: *First*, we will explore correlations between annual patterns of settlement (damselfish) or recruitment (corals) and a number of regional to landscape scale drivers

[e.g., mean sea level (Fig. 2-4), wave climate (Fig. 1-6), other transport processes (e.g., circulation (Fig. 1-7), internal waves (Fig. 2-6), seawater chlorophyll (Fig. 2-4) and water temperature (Fig. 2-4)]. We will expand our analyses of regional to cross-reef transport as mechanisms delivering fish and coral larvae to the lagoon, including extending our molecular approach to additional species of fishes and perhaps corals. *Second*, we will test the effect of landscape-scale drivers that may be impacted by GCC (including internal waves, upwelling) in supplying nutrients to the reef (Leichter & Genovese 2006). This will include an exploration of the relationships between zooplankton supply and reef-associated taxa, with a strong focus on juvenile corals whose success is determined in part by heterotrophic resources (Houlbreque & Ferrier-Pages 2009), particularly during bleaching when autotrophy is depressed (Grottoli et al. 2006). We also will expand our analysis of cross-reef transport as a mechanism delivering larvae to the lagoon, and evaluate the role of internal waves and upwelling (Leichter & Genovese 2006) in supplying nutrients that can affect corals and algae. To continue to forge stronger links between water motion and community structure, we will investigate the possibility of developing molecular markers of coral fecundity that can be used as a non-destructive assay for reproductive status. *Third*, we will explore how recruitment of different coral morphotypes varies across gradients of flow, where larval delivery, growth, and mortality due to corallivory all are related to water motion. We will focus on the performance of juvenile corals, which can inform models to predict coral community structure under different environmental scenarios. *Fourth*, we will continue to investigate how variation in hydrodynamic forcing modulates rates of reef primary production and calcification of key reef organisms and combines with other press drivers (e.g., OA, temperature) to influence growth rates and competitive interactions among reef components (i.e., corals, CCA, macroalgae). These measurements and experiments will lead to predictions of organismal performance and likely 'winners' and 'losers' under different environmental conditions and provide the basis for testable hypotheses about how reef community structure will vary in the future.

THEME 3: EFFECTS OF STRUCTURE – FUNCTION FEEDBACKS ON RESISTANCE AND RESILIENCE

Predicting effects of drivers of ecological change on coral reef communities is made more complex by feedback mechanisms operating through multiple functional pathways and engaging numerous taxa. Ecologically important positive and negative feedback loops between structure and function occur on coral reefs. We know, for example, that increased seawater temperature (press driver) increases coral bleaching and mortality (direct effect), opening up space for algal colonization (indirect effect) and a change in reef community structure; a positive feedback would be increased primary production that might result in a functional / numerical response by herbivores that reduces algal biomass and increases coral recruitment and abundance. Conversely, coral mortality due to physical disturbance reduces structural complexity of the reef and reduces suitable habitat for a wide diversity of species (provisioning function), and thus reduces local biodiversity. This negative feedback could further alter ecosystem function, particularly carbon and nitrogen cycling, by converting reefs from primarily grazing-based to detritus-based systems. Such feedbacks may be common at several scales of organization, from individual coral colonies to entire reefs. Research by MCR investigators indicates that resistance and resilience can be affected greatly by the nature of structure – function feedbacks (Holbrook et al. 2008a, Schmitt et al. in prep.), yet this aspect has received little attention in coral reef ecosystems.

Question 3A: How does resilience vary with the effects of pulse disturbance on the structural complexity of the reef?

Rationale: There are two qualitatively different types of pulse disturbances that kill coral tissue; those that do not affect directly architectural heterogeneity of the reef (coral skeletons left intact; COTS, bleaching, disease) and those that reduce structural complexity (waves, anchor damage). The recent COTS outbreak enables us to explore

how recovery of the fore reef community is affected by these two types of pulse drivers.

Approaches: *First*, the structure treatments (intact or removed) of the long-term experiment will be followed for at least the duration of MCR II to determine the recovery trajectories. *Second*, we anticipate that shorter term experiments and measurements will be designed and implemented as needed to explore underlying causes of major differences in observed trajectories due to the initial difference in structural complexity. Depending on the difference in response, for example, these could include exploration of the effects of spatial heterogeneity on the efficacy of herbivory or early survivorship of coral settlers. *Third*, we plan a close focus on the development of the microbial and *Symbiodinium* consortia that develop on the treatments through time (Figs. 2-2 & 2-3).

Question 3B: How do structure - function feedbacks affect resilience?

Rationale: Branching and massive corals generally conform to the expectation that fast growing species that reproduce both sexually and asexually (e.g., some branching species) should recover faster from a pulse disturbance than slow-growing, sexually reproducing forms (many massive corals). A marked exception in Moorea is the staghorn coral *Acropora pulchra*, an important habitat-forming 'weedy' species. Extensive thickets of staghorn were destroyed on the north and west shores of Moorea by a series of pulse disturbances ~ 25 years ago, but have yet to recover (despite local sources of propagules). A similar situation exists for staghorn corals in the Caribbean (Aronson & Precht 2001). We recently discovered a top-down structure – function feedback involving herbivorous damselfish that farm and guard algae on coral structure that may be key to resilience of staghorn in Moorea (Schmitt et al. in prep.; Fig. 2-8).

Approaches: *First*, we will perform field observations and experiments to understand constraints on recruitment, growth and survivorship of staghorn coral as a function of protection by farmerfish (which also farm on *Porites* spp.), abundance of corallivorous fish, and hydrodynamic regimes. *Second*, we will undertake a landscape-scale study to document historic patterns of occurrence of large staghorn thickets, which can be re-constructed from field surveys and archived images. We then will compare the distribution of historic thickets with the current distribution of farmerfish territories appropriate for the initial establishment of contemporary thickets. *Third*, we will test our understanding of the bottleneck to recovery by out-planting staghorn nubbins to areas deemed suitable and unsuitable by our objective criteria.

Question 3C: How do structure - function feedbacks affect resistance?

Rationale: The provision of nutrients to branching corals may enhance the resistance of a colony to bleaching by, for example, enhancing photosynthesis or altering the *Symbiodinium* or other microbial consortia. While nutrient enrichment can enhance net carbon production of a coral, it can come at the cost of a reduced rate of calcification, suggesting that photosynthesis and calcification compete when there is a limited supply of DIC (Langdon & Atkinson 2005). Damselfish that reside on branching corals provide nutrients and boost coral growth rates (Holbrook et al. 2008a; Fig. 1-13); this accelerated rate of microhabitat provisioning results in larger group size of resident damselfish. This structure – function feedback may enhance resistance of the colony to temperature excursions that trigger bleaching, but may reduce resistance to OA if enhanced photosynthesis lowers calcification when DIC is in short supply. UV can interact with water temperature to cause coral bleaching (Hoegh-Guldberg 1999), and reef organisms produce colored dissolved organic matter (CDOM) that may act as sunscreen. This creates the potential for a community-scale feedback where bleaching-prone taxa gain protection from those that produce CDOM. There also may be an important structure – function feedback involving the production by corals of mucous (a major source of carbon on the reef) and microbial consortia.

Approaches: *First*, at the coral colony scale we will address bottom-up feedbacks between coral-sheltering fishes, branching corals and *Symbiodinium*. We will explore how the feedback varies with flow, how it affects microbes and the composition of

Symbiodinium populations in corals (Stat et al. 2008), and, in mesocosm experiments, whether this affects resistance to thermal stress (bleaching) or OA. We also will explore whether interactions between flow and branching coral morphology influence nutrient retention and abundance of damselfish (via settlement and/or predation), and whether this affects resistance of the colony. *Second*, at a reef-wide scale we are exploring the hypothesis that colored dissolved organic matter (CDOM) produced by reef organisms provides photo-protection, particularly from UV radiation. Little is known about diurnal or seasonal cycles of production of CDOM in coral reef waters, but a possible feedback resulting from climate drivers might be an increase in CDOM production, increasing local photo-protection, and a reduction in coral bleaching. Such effects could feed back to community structure and coral species diversity through the retention of bleaching-susceptible taxa within the community. *Third*, we will investigate how changes in coral community structure alter the production of coral mucous. Coral mucous plays an unknown role in carbon cycling on coral reefs (Wild et al. 2004). We will test hypotheses about the responses of the microbial community to changes in mucous production and availability, which might include both changes in microbial community structure (with concomitant changes in microbial function [e.g., respiration, nitrate assimilation / reduction]) and/or changes in the rates of microbial function. Such changes could have feedback effects on community structure by altering abundances of taxa that rely on microbes directly (as food), or indirectly as the result of organic matter remineralization, which could affect the resistance of the assemblage.

INTEGRATION AND MODELING

An ongoing challenge is the need for integration among studies and biological processes, a task complicated by the non-linear interdependence of many coral traits and their strong responses to a diversity of physical drivers. In MCR I we began developing two sets of models to facilitate integration and extend results. The first uses Dynamic Energy Budget (DEB) theory to model a symbiotic mixotroph (Muller et al. 2009a, b), which specifies the flows of matter and energy among the host coral, its symbiont *Symbiodinium* and the environment. The DEB approach was complemented by ODE models focused on aspects of population and community dynamics. The second body of models describes fundamental physical oceanographic processes that influence the structure and function of coral reefs in a variety of ways. We will incorporate GCC drivers into our DEB models of coral, develop techniques to scale up to higher levels of ecological organization, and increasingly couple biology to our physical oceanographic models. Below we describe MCR II modeling and integration.

Ecological Modeling and Integration. To help develop a unified body of theory and models to support projects and facilitate synthesis, we focused on an approach that describes the flows of both energy and elemental matter within organisms and between organisms and their environment. This approach is *Dynamic Energy Budget* (DEB) theory (Kooijman 2010), though for our applications, the flows of key elements (C, N, Ca) play a larger role than energy. In DEB models, assimilated energy is stored and then utilized for growth, maintenance and reproduction; flow of elemental matter is calculated from knowledge of the stoichiometry of the components. We developed the first DEB model for a coral-algal symbiont system (Fig. 1-5) (Muller et al. 2009a, b), and have used it and other constructs to explore the damaging effects of high irradiance and to project the functional significance of changing *Symbiodinium* types (Baskett et al. 2009). The emerging approach will help synthesize results within our GCC/OA theme of MCR II. We will expand the model to incorporate the flux of Ca_2^+ and HCO_3^- to understand how OA may affect the growth of corals under a diversity of physical conditions (e.g., light, temperature, flow).

We plan to expand our suite of analytical (e.g., ODE) models of *population dynamics* of key organisms, *species interactions* and *food webs*. For example, we will explore the utility of epidemiological models for understanding COTS dynamics. A

strong foundation of empirical information and modeling work on COTS exists, including non-spatial population and predator-prey models, and spatial models of seastar aggregation and larval transport (Reichelt et al. 1990). We will focus our theoretical efforts on key identified gaps in existing modeling efforts (e.g., persistence of COTS at low densities, outbreak triggers, spatial dynamics, and habitat structure). With respect to species interactions and food webs, we have begun to develop models of Intra-guild Predation (IGP) in structured environments based on the branching coral – damselfish – predator system that we have explored experimentally (e.g., Schmitt et al. 2009) and which will be used to examine structure – function feedbacks (Theme 3). Results from the simplest (ODE) model of this IGP system (assuming spatial homogeneity) will be compared to more complex (spatially explicit, stochastic) models that include a number of more realistic features of the system, including spatial heterogeneity and disparate spatial scales of the various interacting species. Such a model could be used to investigate the community consequences of removing top predators (e.g., overfishing), of variation in productivity of the system, or of OA on reducing coral calcification (growth) rates. In addition, we will explore the feasibility of using a systems biology approach to model the branching coral – fish – *Symbiodinium* system, with a goal of eventually incorporating IGP, flow and other factors that we discover influence dynamics of this web of interacting species. Finally, we will develop qualitative and statistical models (e.g., structural equation models) to further explore food webs, and as a tool for generating hypotheses regarding responses of coral reefs to external drivers.

Modeling Physical Processes and Biological-Physical Coupling. Coral reefs are physically-forced systems so a continuing focus of MCR II will be to model important hydrodynamic and abiotic features that operate over a range of spatial and temporal scales. We will emphasize integration of physical and biological measurements and models to gain better predictive understanding of the function and dynamics of coral reefs. In marine systems, materials are transported by water flow, and we have developed a series of models to describe hydrodynamic processes over relevant scales. At the scale of 100s of kms, we have measured *propagating mesoscale flow structures* that produce island-wide fluctuations in sea level, similar to the tidal amplitude (~ 0.1m) but magnified by ~ 50% in the back reef, that last ~ 2 weeks. By altering water levels on the fore reef, these low-phase mesoscale sea level perturbations (MSLPs) can modulate the effects of breaking waves and current flow behind the reef crest. We plan to build models to investigate the contribution of MSLPs to observed differences in coral growth rates and morphologies on the reef crest relative to the lagoon (Edmunds & Lenihan 2009, Lenihan et al. submitted, Lenihan & Edmunds in revision) as well as on observed vertical patterns of zooplankton distributions (Alldredge & King 2009).

At the island scale, we have observed that *longshore currents* around Moorea exhibit tidal oscillations with peak velocities of 10 to 40 cm s⁻¹. Multi-day averages of mean current velocities also show persistent flows of roughly 2-4 cm s⁻¹ in a counter-clockwise, alongshore direction around the island (Fig. 2-7). This yields a calculated time of 15-30 days for the implied circum-island flow, approximately the same time scale as the planktonic larval duration for many fishes and invertebrates. We plan to construct general models of this alongshore current to help predict potential patterns of larval retention / dispersion. This will serve as an important next step in our attempts to link observed patterns of genetic relatedness in several species of fishes (Leray et al. in press, Leray et al. 2009, Bernardi et al. 2003) with island-scale flow characteristics.

The nearshore *wave climate* around Moorea shows persistent seasonal variation in measured significant wave heights (maximum ~ 10 m) and calculated values of wave power. Large waves with long periods drive correspondingly strong currents behind the reef crest in the lagoons (Hench et al. 2008; Fig. 1-7). We will use statistical models incorporating observed variation in wave height and power to explore possible linkages with models of coral settlement developed from measurements made at back reef sites

around the island. Coral settlement data (Adjeroud et al. 2009) suggest that differences in the timing of strong, cross-reef transport between winter and summer may interact with differences in the timing of coral larval availability among Acroporidae and Poritidae. The interactions between lagoon currents and larval availability could partially explain family-level patterns in coral settlement among the shores of Moorea.

With respect to *lagoon circulation*, for MCR I we used simple 1-D models to understand and predict reef and lagoon water velocities and water levels from offshore wave forcing (Hearn 1999, Gourlay & Colleter 2005, Hench et al. 2008). For MCR II, we plan to implement a 3-D time-stepping circulation and wave model (Booij et al. 1999) to interpret spatial and temporal patterns in time series and other MCR ecological datasets (e.g., spatial settlement patterns of fish and invertebrates, distribution of coral morphologies). The circulation model also will be used to estimate spatial distributions of water residence times (Zimmerman 1988), and how they vary with changes in local forcing (e.g., sustained easterly trade winds vs. southerly Maramus). For example, a recent modeling study of Kaneohe Bay, Hawaii showed lagoon residence times ranged from <1 day to >1 month (Lowe et al. 2009) depending on location. We also plan to use the model as the basis for particle tracking studies (e.g., Hench & Luettich 2003) to explore questions of transport, retention, connectivity, and disturbances. We anticipate that the circulation model eventually will be a key component of an emerging algorithm for predicting temporal and spatial variation in reef metabolism in lagoons of Moorea.

Nutrients and particles (including larvae) can be moved onto the reef via *internal waves* (Fig. 2-6). Five years of continuous time series measurements of bottom temperature reveal significant influence of internal waves on the fore reef slopes. These data will be used to calculate the coherence and time lags of signals around the island in an effort to model the source(s) of internal wave generation and direction of propagation. The potential input of dissolved inorganic nutrients to the reef slope ecosystem will be modeled using relationships between water column temperature and nutrients measured in the offshore water column. A conceptual model of the potential impact of mesoscale sea level fluctuations on thermocline depth will be tested by examining relationships between the time series of sea level and measured depth stratification of temperature. A persistent feature in the bottom temperature time series observations is a strong and abrupt seasonal modulation of thermal variation observed at depth on the reef slopes. A goal of the modeling will be better understanding of the mechanisms controlling the seasonal variation of internal wave impacts.

At the scale of individual coral colonies, we are modeling *small-scale flows* around and through corals to help understand how hydrodynamics, coral morphology and resident fish interact to affect coral growth. This work will integrate with several ecological modeling efforts (see above). Coral growth rates can be affected by hydrodynamics in several ways. Shorter residence times associated with faster flow and more open colony morphologies result in greater mass transfer (Reidenbach et al. 2006) and higher coral respiration rates (Bruno & Edmunds 1998). Faster flows also result in thicker branches and less open colony morphologies (Mass & Genin 2008). Long residence times can be beneficial for corals when the colony is occupied by sheltering damselfish. Fish excretion increases concentrations of ammonium within a colony, which in turn can increase coral growth (Holbrook et al. 2008a); the less open the coral, the longer the residence time, and the more fish enhance growth (Fig. 1-13).

Finally, we use a suite of bio-optical models to retrieve *biogeochemical data* on local to regional scales from satellite ocean color data. We have developed a model that simultaneously retrieves the sub-surface Chlorophyll concentration, the sum of the dissolved and detrital matter absorption coefficient and the particulate backscattering coefficient from *in situ* or satellite ocean color data (Maritorena et al. 2002, Maritorena & Siegel 2005). We plan on developing the bio-optical and other models further to look at additional biogeochemical variables (diffuse attenuation, fluorescence, particle size distribution, Raman scattering) around Moorea from satellite ocean color data. We

already have developed some preliminary models (e.g., Kostadinov et al. 2009). We will use variation in these parameters, together with hindcast estimates for potentially relevant oceanographic conditions, to explore, for example, correlations in interannual variation in daily settlement of larvae of a focal reef fish (currently a 17 year time series).

CROSS-SITE & NETWORK ACTIVITIES

MCR personnel will remain active in a variety of LTER Network activities, including membership on NISAC, the Science Council and the Network Student Group (MCR will cycle off the LTER Executive Committee in 2010). We will continue to participate actively in EcoTrends and other LTER working groups (e.g., Web Services, Remote Sensing, State Change) as well as LTER All Scientists Meetings. UC Santa Barbara is the lead campus for both the SBC and MCR LTER sites, providing rich opportunities for synergism as 7 investigators are involved with both projects. Cross-site activities will include participation in each other's annual meetings, joint graduate seminars and close collaboration in information management and development of web site tools. Continuing MCR-SBC research projects include modeling of phase shifts in temperate rocky reef and coral reef ecosystems, studies of the role of internal waves in supplying nutrients to nearshore reef ecosystems, effects of OA on ecosystems with structure-forming foundational taxa, and a socioeconomic project comparing fisheries management. We will initiate a modeling effort to compare effects of disturbances on foundation species (giant kelp, coral) and their associated food webs in the two ecosystems. We also have been in discussion with CCE regarding mutual interests and possible collaborations.

MCR will continue its collaboration with an international group of scientists, including those from other LTER (NTL, FCE, ARC, MCM, SBC) and ILTER (Kenting Coral Reef and Yuan Yang Lake in Taiwan) sites and agencies (NOAA) to develop real-time sensor networks on coral reefs (CREON, <http://www.coralreefeon.org/>) and lakes (GLEON, <http://www.gleon.org/>), and to promote scientific research motivated by network-level science questions. Major international partners for CREON are the Kenting ILTER site, the Australian Institute of Marine Science and three Australian universities (Melbourne, James Cook, Queensland), with cyberinfrastructure development led by groups at CalIT2 (UC San Diego) and the National Center for High Speed Computing (Hsinchu, Taiwan). The SBC and MCR sites will continue to work together on joint deployments of real-time sensors for use on instrumented moorings on both tropical and temperate reefs. MCR will expand on our growing set of research collaborations (particularly in coral physiology and molecular biology) and student - investigator exchanges with the National Museum of Marine Biology and Aquarium, Taiwan, where the Kenting Coral Reef ILTER site is located. We also will continue our collaborative research program with scientists at James Cook University in Australia. We also have initiated and will develop further collaborations with European coral reef scientists from the Laboratoire d'Océanographie de Villefranche, Musée Océanographique de Monaco and IRD (Institut de Recherche pour le Développement) that complement our ongoing interactions with French scientists on Moorea associated with CRILOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement), operated by EPHE (l'Ecole Pratique des Hautes Etudes), CNRS (Centre National de la Recherche Scientifique) and the University of Perpignan.

SYNTHESIS

The research we propose for MCR II addresses the dynamics of coral reef ecosystems in the context of long-term environmental drivers and short-term disturbances. Coral reefs are the most diverse of all marine ecosystems by far, supporting, for example, a third of all species of marine fishes (Moberg & Folke 1999) despite covering a tiny fraction (< 0.2%) of the ocean floor (Birkeland 2001). They also rank at the top in terms of gross primary productivity in the ocean - much of which arises from tight recycling of chemicals between algal symbionts and corals, with very little of the carbon exported

from the ecosystem (Birkeland 2001). From an economic viewpoint, corals reefs yield upwards of \$375 billion annually in goods and services, an astonishing figure given the rarity of the ecosystem (Moore & Best 2001). Coral reefs also rank among the most vulnerable of marine ecosystems to Global Climate Change. The algal symbiont of coral (*Symbiodinium*) is near its thermal tolerance limit, and even brief excursions of seawater temperature can cause widespread bleaching of corals; the massive, world-wide bleaching episode of 1987-88 brought into sharp focus the threat from rising seawater temperature. Until recently, the warming ocean was viewed as the primary driver of change in coral reefs arising from Global Climate Change. Carbonization of the ocean from increasing $p\text{CO}_2$ in seawater (Ocean Acidification) is now recognized as a GCC driver that may have effects as great or greater than warming, and together are likely to cause sweeping changes in the coming decades. In MCR II, we will begin to explore the effects of OA on coral reefs and its interactive effects with temperature and other press drivers. Short-term disturbances such as storm waves or pest outbreaks are occurring against a changing background of seawater temperature and chemistry, which highlights the need to understand factors that affect resistance and resilience to disturbances. We anticipate that understanding how climate and disturbances affect coral reefs will be a long-term focus of the MCR. Ocean Acidification and rising seawater temperatures in particular will become important GCC drivers to the other marine sites in the LTER and ILTER networks.

RESPONSE TO MID-TERM REVIEW

The mid-term review, conducted in July 2007, did not include recommendations for immediate corrective action. It did contain seven suggestions regarding site science for consideration at renewal. Two suggestions urged development of a more explicit 'conceptual roadmap' to better connect long-term drivers and disturbance regimes to our studies. We adopted the unifying conceptual framework in the LTER decadal plan and operationalized it for the MCR; we believe this is an ideal construct to make these linkages more explicit. Another suggestion was to complement our DEB modeling approach with other models that address hydrodynamics and flows of key materials. We have included these modeling and integration activities in MCR II. A fourth suggestion was to consider expanding our time series program to obtain additional samples of certain water column properties. We will expand our sampling of water chemistry related to OA. The review team suggested increased sampling of nutrients, and we immediately did this following the review in 2007; however, based on analysis of the data and our needs, we will scale back nutrient sampling in the MCR II time series program and focus on processes and events that inject nutrients into the reef system. A fifth suggestion was to expand coverage of hydrodynamic observations to further offshore to measure cross-shore gradients in physical forcing. To do this, we began analyzing data from the Toga/Tao buoy array and other sources to explore connections between distant low frequency variability and local lagoon hydrodynamics; this effort uncovered the mesoscale sea level perturbations that produce low frequency sea level changes around Moorea. A sixth suggestion was to obtain detailed bathymetry of Moorea using LIDAR or other approaches. The high cost associated with LIDAR in Moorea dictates we obtain substantial extramural support for this approach, and our efforts to date have not been successful. French scientists recently made bathymetry measurements of the fore reef of Moorea, and we are determining whether we can obtain that information. Meanwhile, we have initiated a low-cost method to measure bathymetry within lagoons, with an initial focus on the north shore. The final suggestion was to consider tapping paleoecological information in coral skeletons, etc. as proxies of environmental variables to obtain longer term perspectives. We received LTER supplemental funds for two such studies that are underway.

Figure 1-1. Moorea, French Polynesia, is in the central South Pacific **(A)** 17 km west of Tahiti **(B)**. It is a triangular shaped high island encircled by a barrier reef that forms shallow, narrow lagoons **(C - E)**; the fore reef **(F, G)** drops off steeply just seaward of the reef crest **(E)**. Time series samples are taken and oceanographic instrument deployments occur in three habitats at each of six sites (LTER 1 – 6) around the island **(D)**. Virtually all coral on the fore reef has been killed by an outbreak of crown-of-thorns seastars (COTS) since image **(G)** was taken in 2006 (see Fig. 1-2).

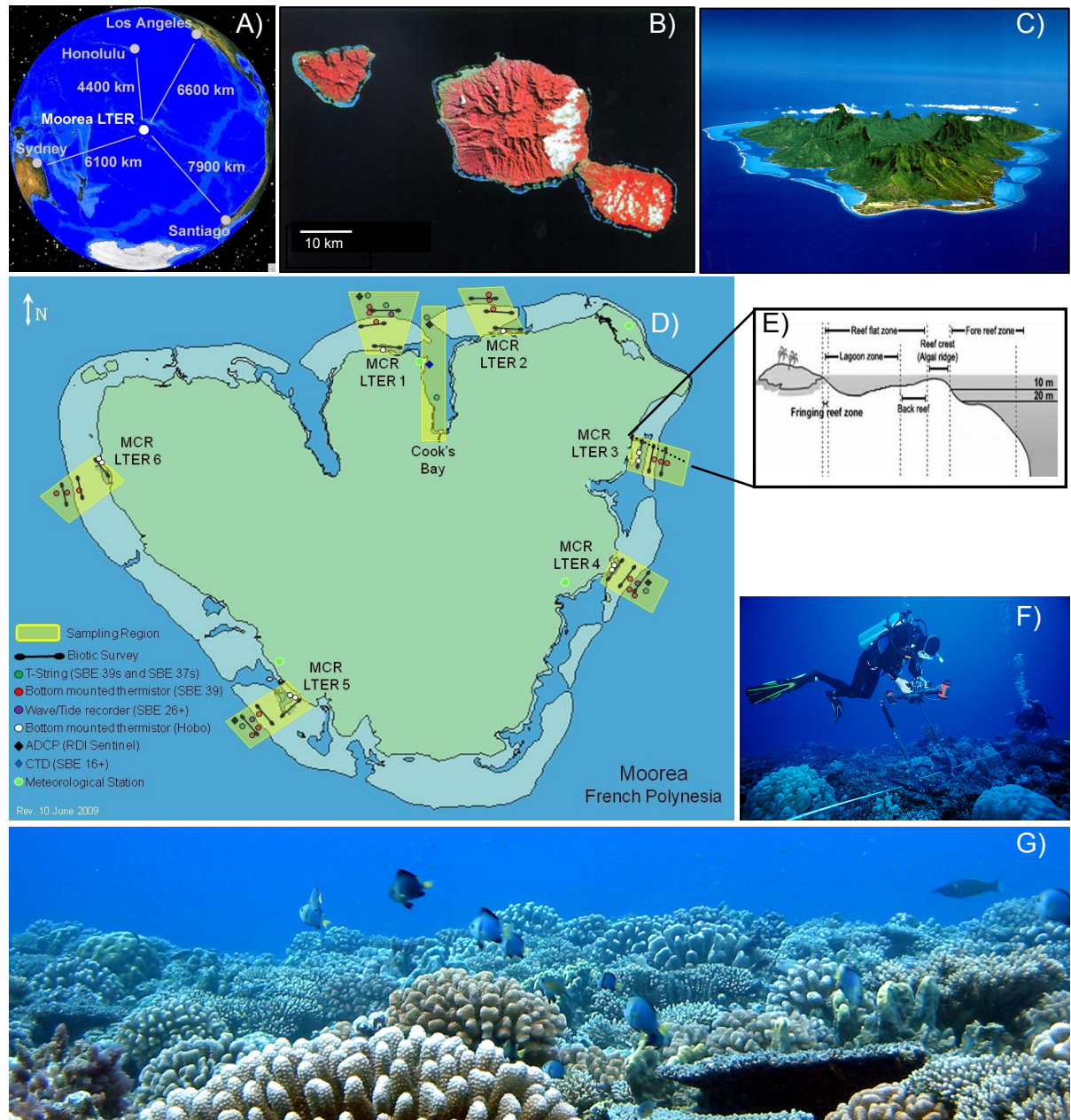


Figure 1-2. (A) History of bleaching and cyclone disturbance events at Moorea from 1991 to 2006 (Adjeroud et al. 2009). A COTS outbreak in 2007-09 **(B)** resulted in a 90-98% decline in coral on the fore reef **(C)** and about a doubling in macroalgal cover **(D)**. Fishes that reside in coral declined with early losses of branching species **(E)**, and herbivorous fishes may be responding positively **(F)**. Similar patterns were observed at 10 m on the fore reef, but not on fringing reefs (not shown).

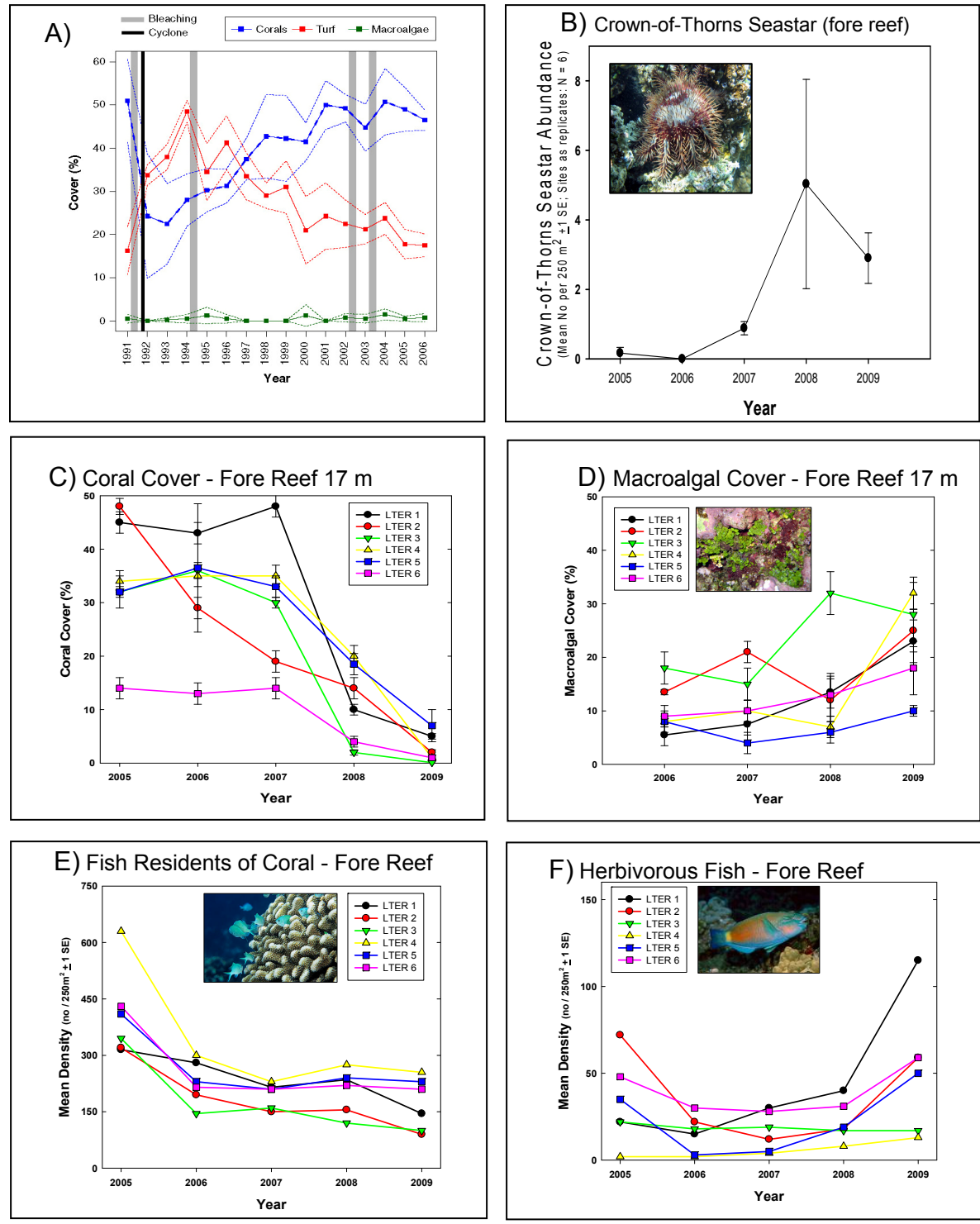


Figure 1-3. Experiments with *Porites* corals revealed that acclimatization affected the response to thermal stress for massive *Porites*, but not *Porites irregularis*, with the effects of high temperature most acute in corals previously grown under low temperature and shade. Nubbins were exposed for 15 days to combinations of cool and shady conditions, and then transferred to conditions that contrasted the effects of ambient and high temperature (31°C).

Subsequent thermal stress

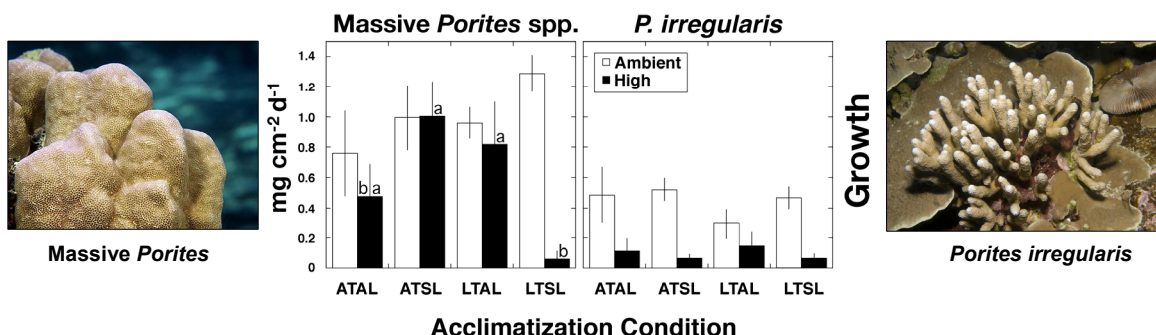


Figure 1-4. Greater apparent resilience of massive *Porites* corals may be related to their thick tissue that penetrates deeply into the skeleton. Vertical stratification of *Symbiodinium* within *P. lutea* (A) is accompanied by phenotypic differences in photophysiology: rETR performance in inner tissues responded to increasing light differently from those in outer tissue (B & C). Genetic analyses (D) revealed that the algae were virtually identical throughout the tissue (all clade C15).

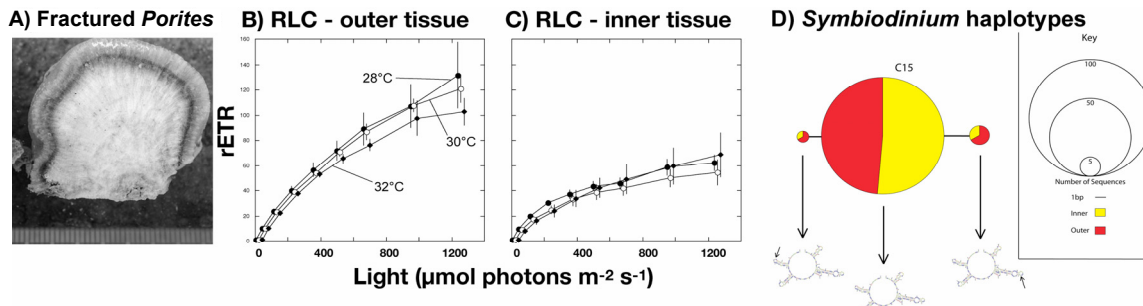


Figure 1-5. DEB Coral – *Symbiodinium* model depicting flow of fluxes among environment (blue), host (white) and symbiont (green) (Muller et al. 2009a). Circles represent synthesizing units (SU) and boxes are biomass compartments. Broken lines are fluxes producing carbon dioxide and ammonia, i.e., the fluxes designating maintenance and overheads of assimilation [energetic cost to convert one type of compound (food or reserves) into another (reserves or structure)] and growth. Carbon dioxide and ammonia thus produced are recycled, notably by the photosynthesizing and assimilation SUs. In this way, nitrogen in the food source of the host is made available to the symbiont. Excess carbon dioxide and ammonia are excreted, i.e., the internal pools of these compounds are kept negligibly small.

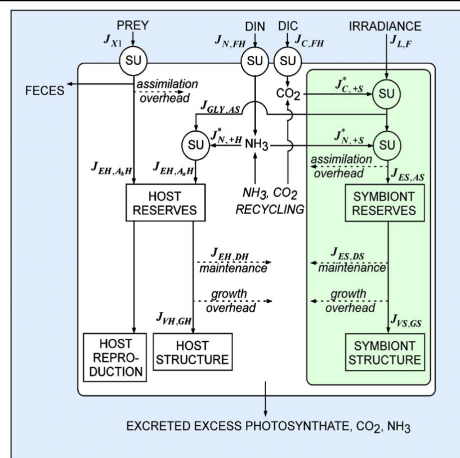


Figure 1-6. Offshore wave climate. **(A)** Time series of wave height (black) and period (green) around Moorea from 2005 through 2008 as measured by bottom pressure sensors (SBE 26+ & ADCPs) at MCR LTER Sites 1, 4 and 5 (insert). Red dashed line indicates significant wave heights (average of upper third of wave heights) H_s of 4 m; black dashed line indicates 12 sec periods (waves with periods ≥ 12 sec are deep ocean swell; waves with periods < 10 s are local wind waves, which are more common on the N side). Highest waves and longest period waves are on the SW side of Moorea. The wave burst on 1 Nov. 2007 (red arrow) had very high individual waves, which is shown in detail for LTER Site 5 **(B)**; wave photograph was taken at nearby Teahupoo during an international surfing event on Nov. 1, 2007.

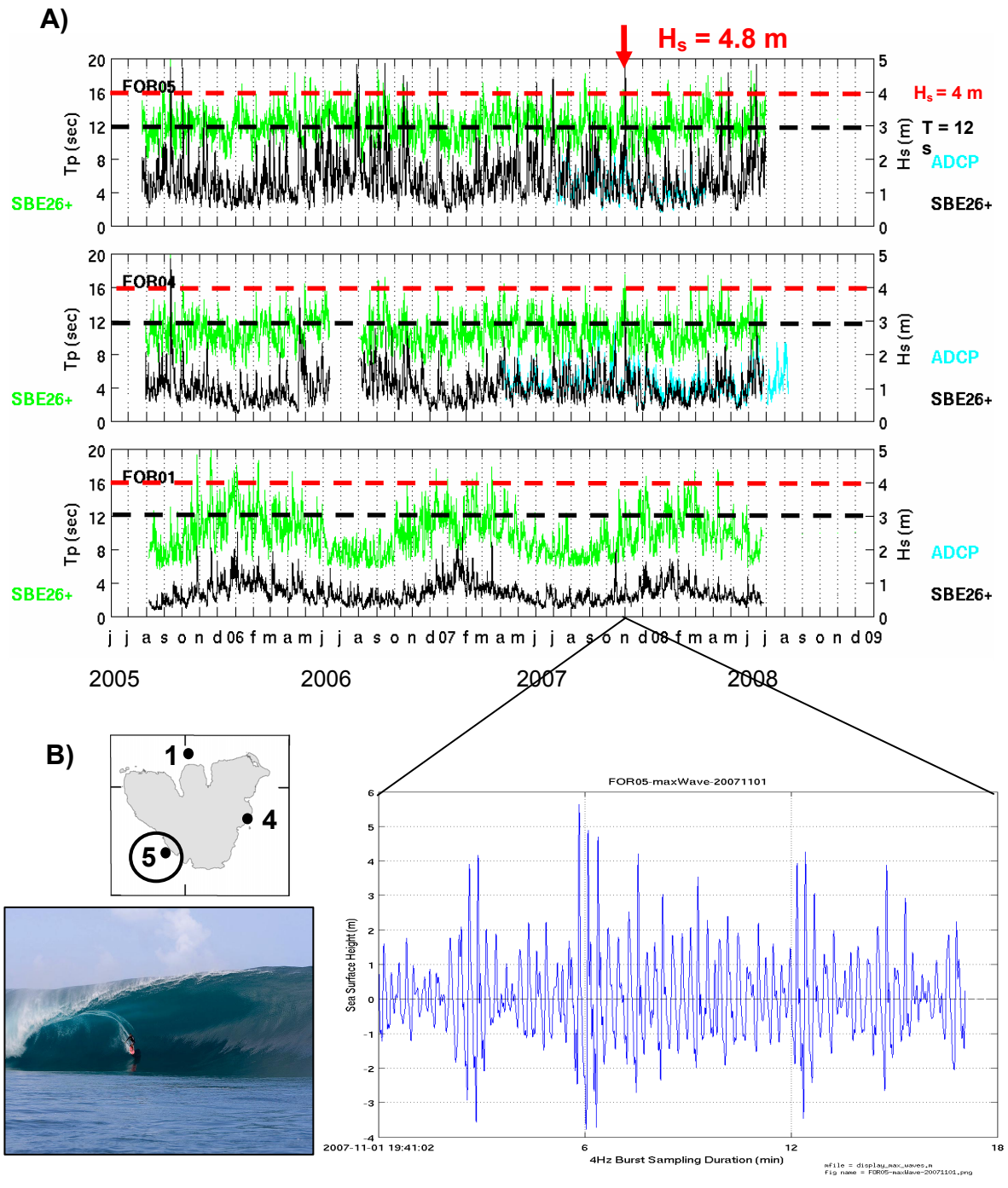


Figure 1-7. North shore (A) lagoon circulation. Flow speed and direction were measured (B) to estimate Eulerian mean currents (C) and circulation features (D). Water entering over the reef crest moves across the back reef and exits through a pass, forming km-scale circulation cells.

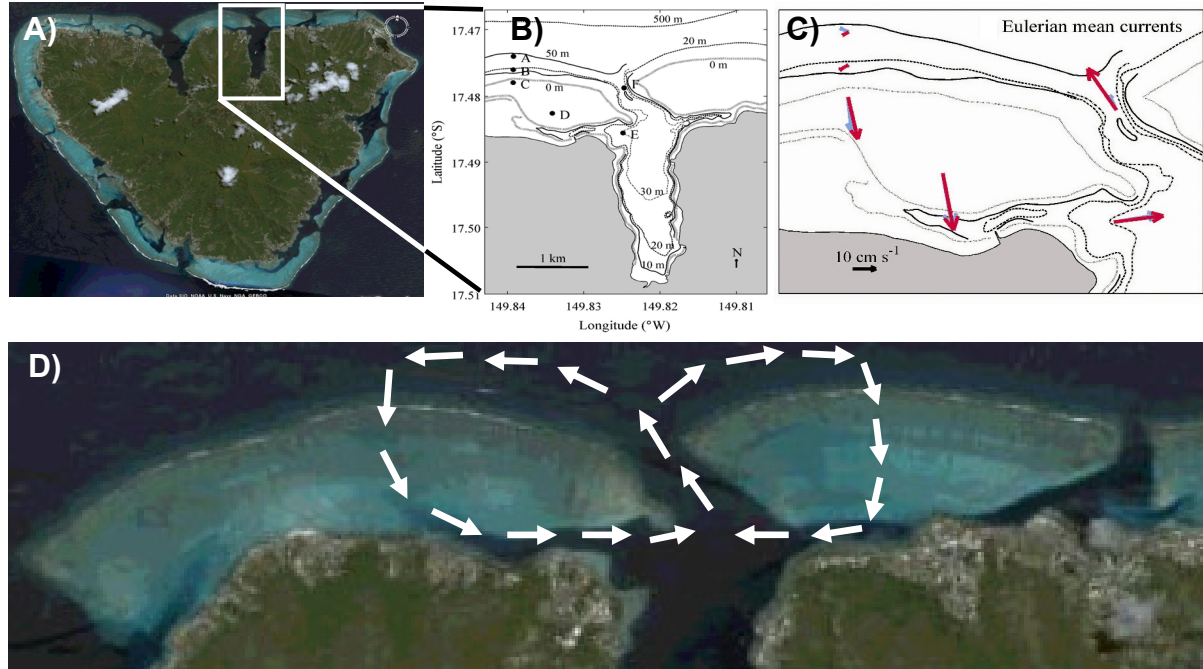


Figure 1-8. Mesoscale Sea Level Anomalies. (A) Snapshot of regional variation in sea level showing position (arrow) and latitude (dashed line) of Moorea. (B) Time series of regional sea level anomalies that propagate westward past Moorea (dashed line) from mesoscale flow eddies in the open ocean due to the rotation of Earth. (C) Corresponding time series variation in sea level measured by MCR LTER instrumentation at various sites around Moorea [dashed line in (B)].

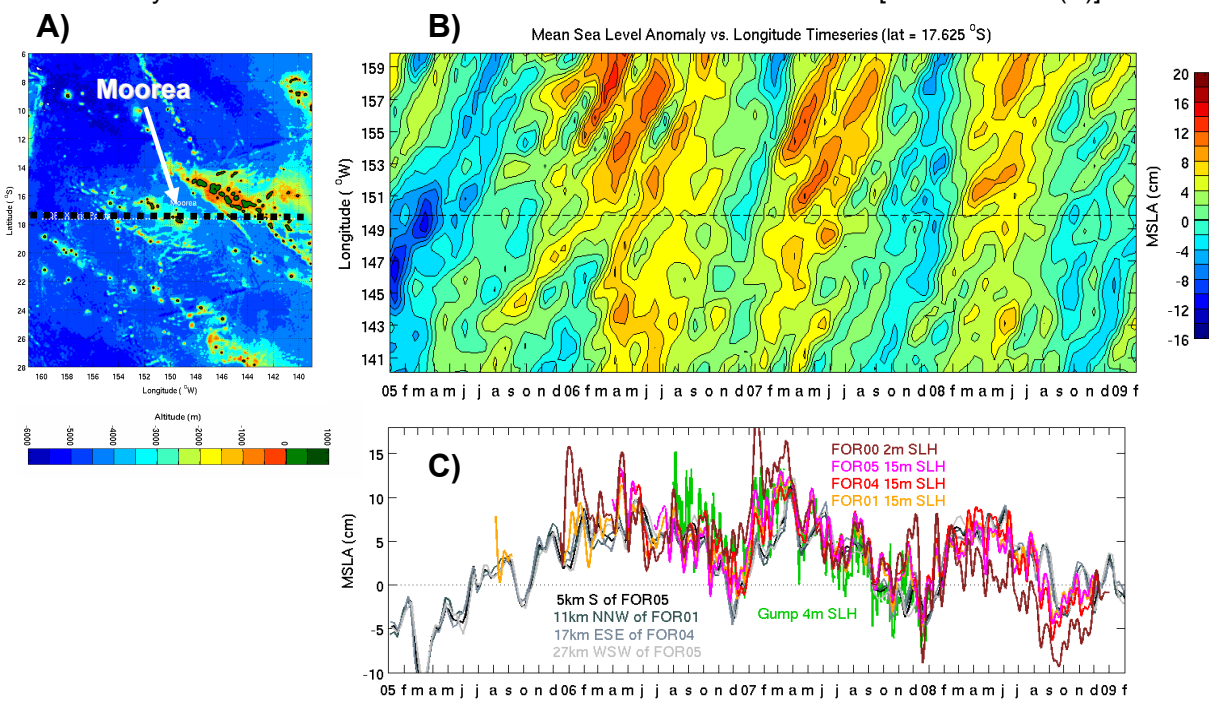


Figure 1-9. Effects of flow and light on Net Primary Production (NP) on the reef. **(A)** Root mean square (RMS) flow speed (black) and net primary production (red) over the reef at LTER 1 in late January 2007 (austral summer). Tidal-related differences in hydrodynamics result in co-variation of light and flow during the day, centered around solar noon (sun symbol). **(B)** NP as a function of light availability during austral summer (Jan. 07). I_k is the saturation irradiance. NP is light-saturated for a much higher proportion of the day during summer than winter.

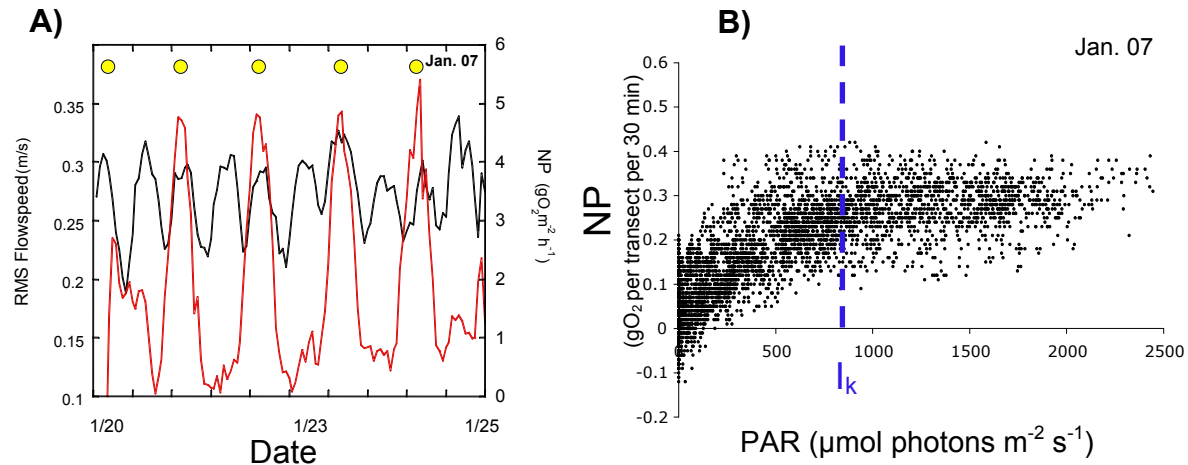


Figure 1-10. Seasonal and annual trends in benthic **(A)** and water column **(B)** primary productivity. **(A)** Mean rates of NP (\pm SE) over the back reef at LTER 1 (blue bars), suggesting a monotonic decline in seasonal rates (numbers = # days on which NP estimated). Inset shows mean (\pm SE) percent cover of major benthic components in June 2009. **(B)** Mean primary production and chlorophyll a in the water column (depth averaged) on the north shore.

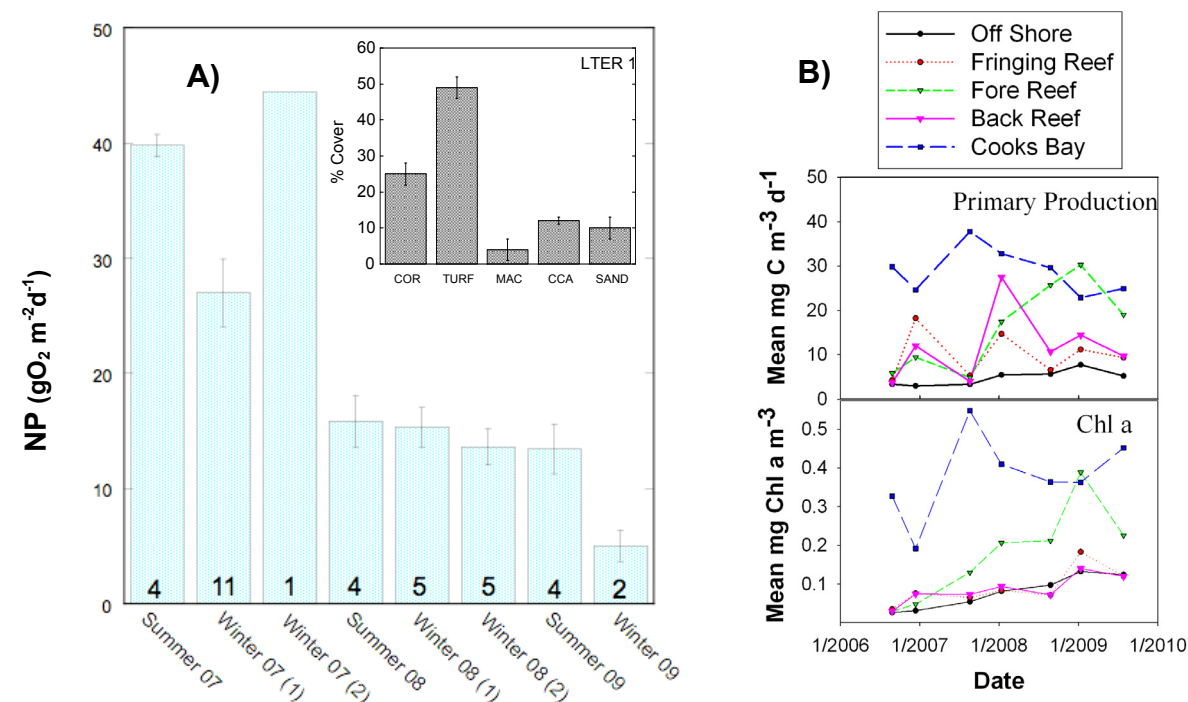


Figure 1-11. Concentration of nutrients (center: nitrate + nitrite; right: phosphate) in the water column above various reef habitats as a function of nutrient concentrations 5 km offshore. (Photo) MCR investigators collecting a seawater sample by deploying a Niskin bottle from a small boat.

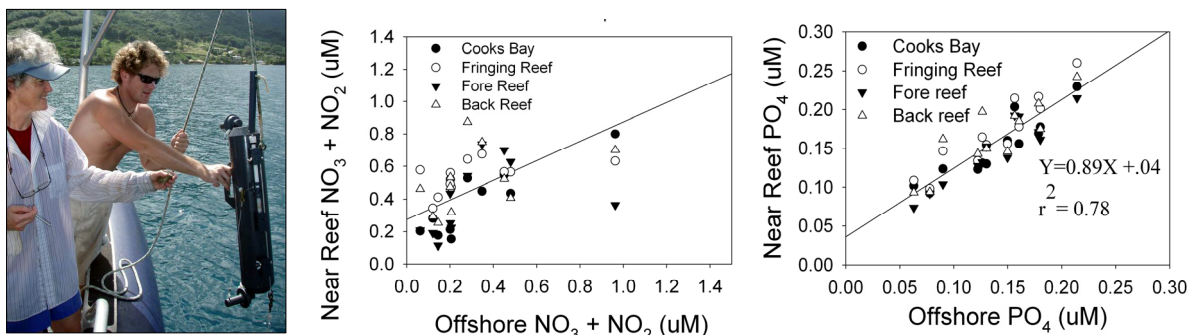


Figure 1-12. Biophysical coupling of predation, flow and seawater temperature on coral. Experimental colonies of massive *Porites* subjected to investigator-imposed damage to mimic corallivory (A) were allowed to recover for 10 days in treatments that crossed flow speed (6, 21 cm s^{-1}) and temperature (27° , 30°C) to assess effects on skeletal growth (B) and photophysiology (C). Growth was affected by temperature but not flow, while photophysiology (outside the damaged area) was influenced by temperature, flow and damage.

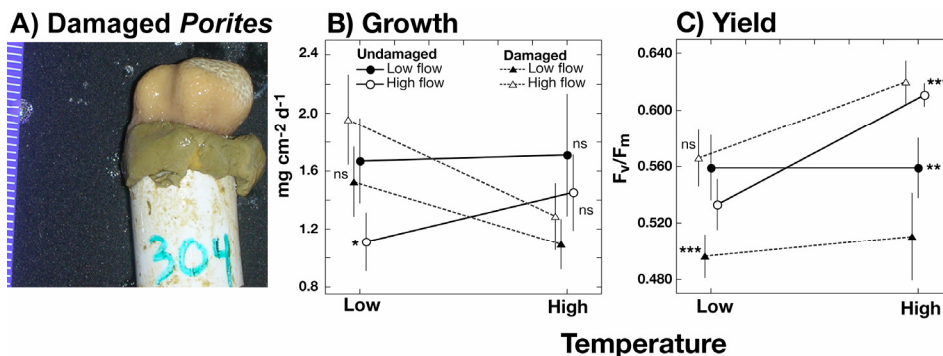


Figure 1-13. Growth enhancement of *Pocillopora* by sheltering damselfish. Increases in fish biomass increased coral skeletal growth (A) and concentrations of ammonia (B). Studies using labeled fish food showed corals incorporated ammonia excreted by damselfish (C). Openness of a coral colony affected washout rates of ammonia (D), and together the biomass of resident fish and colony openness explained 76% of variation in coral growth. Larger corals have more fish.

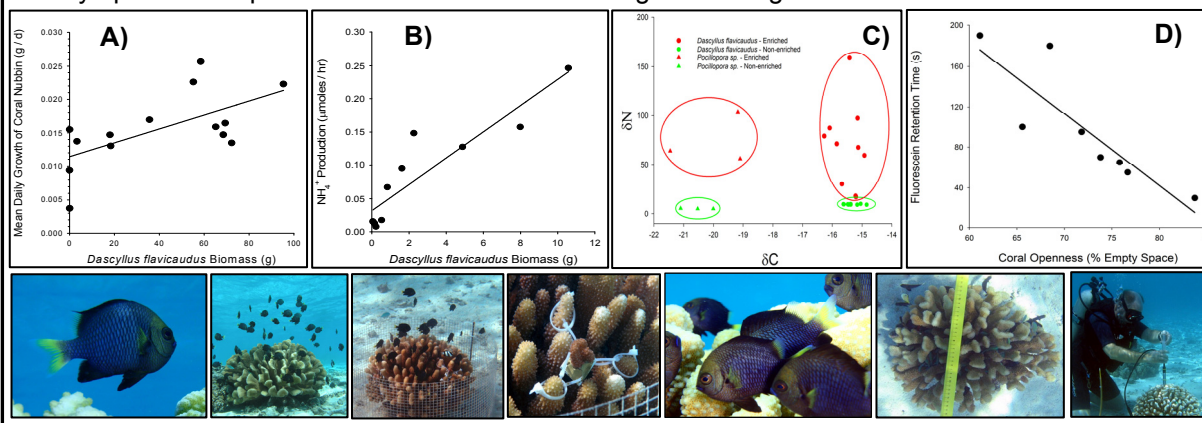
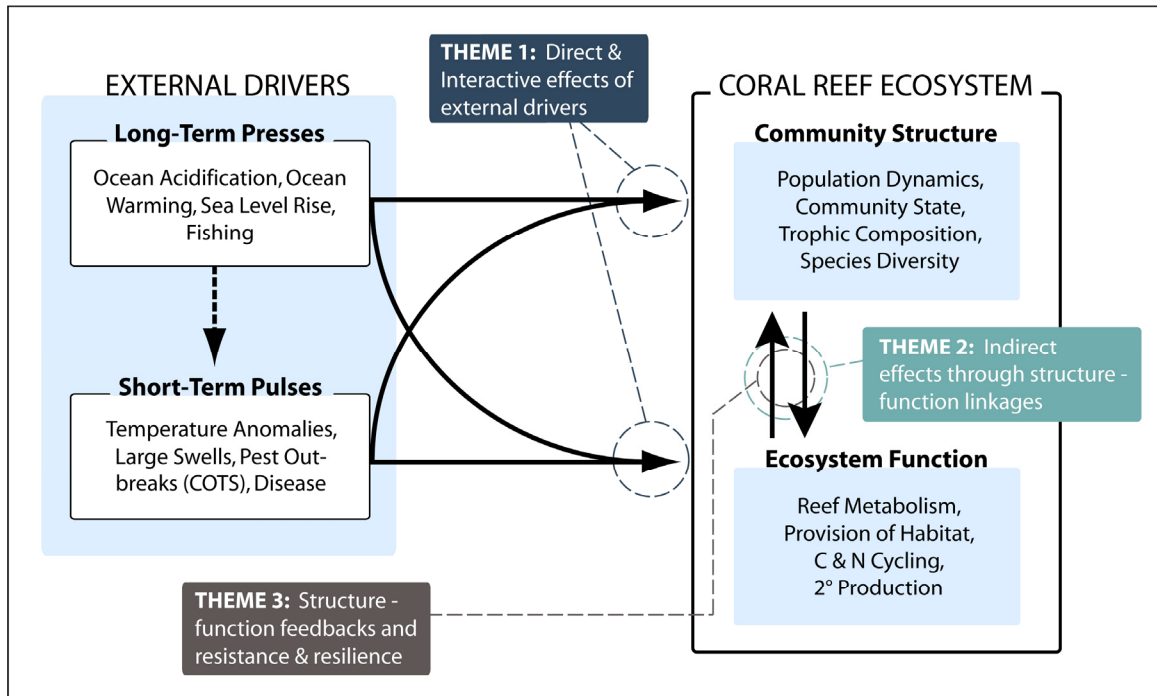


Figure 2-1. The conceptual framework, adapted from the LTER decadal plan (US LTER 2007), for the MCR II research program. Research questions are organized under three themes that make explicit the direct, interactive and indirect linkages between press and pulse drivers and the coral reef ecosystem. The themes and specific questions are shown below. Projects within each theme, together with the key associated investigators, are given in Table 2-1; our research synthesis schema and management structure are given in Figure 3-1.



THEME 1: INTERACTIVE EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION

Question 1A. What is the nature of the functional responses by foundation taxa to major Global Climate Change drivers?

Question 1B. What are the synergistic effects involving Ocean Acidification and seawater temperature on key metabolic processes?

Question 1C. How do pulse drivers interact with a key press driver (fishing) to influence community structure?

THEME 2: INDIRECT EFFECTS OF PRESS AND PULSE DRIVERS ON STRUCTURE AND FUNCTION

Question 2A. How do changes in community structure affect ecosystem function?

Question 2B. How do changes in ecosystem function affect community structure?

THEME 3: EFFECTS OF STRUCTURE - FUNCTION FEEDBACKS ON RESISTANCE AND RESILIENCE

Question 3A. How does resilience vary with the effects of pulse disturbance on the structural complexity of the reef?

Question 3B. How do structure - function feedbacks affect resilience?

Question 3C. How do structure - function feedbacks affect resistance?

Table 2-1. Summary of proposed investigations and key scientists for each MCR II research question. Figure 2-1 shows the themes and how they relate to our conceptual framework, and Figure 3-1 shows our schema for integrating the research program and our management structure.

THEME 1 - Question 1A. What is the nature of the functional responses by foundation taxa to major Global Climate Change drivers?	
1. Edmunds/Carpenter	Calcification of corals and algae in response to OA
2. Fabry/Aldredge	Dissolution of corals and carbonates in response to OA
3. Hofmann	Mechanistic basis of organismic response to interactive effects of GCC
4. Edmunds/Gates	Acclimatization and adaptation of corals to GCC
5. Nisbet/Edmunds	DEB modeling of the response of corals to GCC drivers
THEME 1 - Question 1B. What are the synergistic effects involving Ocean Acidification and seawater temperature on key metabolic processes?	
6. Edmunds/Carpenter	Interactive effects of OA and temperature on calcification of corals and algae at organismic and community scales
7. Fabry/Aldredge	Interactive effects of OA and nutrients on coral reef dissolution
8. Carlson	Microbial community dynamics and C-cycling
9. Williams	OA effects on N-fixation and cycling
THEME 1 - Question 1C. How do pulse drivers interact with a key press driver (fishing) to influence community structure?	
10. Schmitt/Holbrook/Brooks/Carpenter/Edmunds	Long-term experiment – ecosystem manipulation to explore trajectories following COTS disturbance
THEME 2 - Question 2A. How do changes in community structure affect ecosystem function?	
11. Hench/Leichter/Carpenter	Hydrodynamics & reef community structure and function
12. Brooks/Schmitt/Holbrook/Carlson	Flow, coral morphology, sheltering fishes & interstitial microbial communities
13. Briggs/Holbrook/Schmitt/Brooks	Modeling coral reef fish communities
14. Lenihan/Hench	Corallivory and coral recruitment across gradients in flow
THEME 2 - Question 2B. How do changes in ecosystem function affect community structure?	
15. Bernardi/Edmunds/Washburn/Aldredge/Hench	Hydrodynamics, propagule/zooplankton flux and community structure
16. Leichter/Gates/Edmunds	Water motion/coral fecundity, upwelling/nutrient delivery and community structure
17. Lenihan/Hench	Coral recruitment, corallivory, and juvenile coral performance
18. Hench/Leichter/Carpenter/MacIntyre	Hydrodynamic forcing of reef metabolism – effects on community structure
THEME 3 - Question 3A. How does resilience vary with the effects of pulse disturbance on the structural complexity of the reef?	
19. Schmitt/Holbrook/Brooks/Gates/Carpenter/Edmunds/Carlson	Long-term experiment – resilience and trajectories of the <i>Symbiodinium</i> and microbial communities
THEME 3 - Question 3B. How do structure - function feedbacks affect resilience?	
20. Holbrook/Schmitt/Brooks	Recruitment, growth, and survivorship of staghorn coral
THEME 3 - Question 3C. How do structure - function feedbacks affect resistance?	
21. Schmitt/Holbrook/Brooks/Gates/Briggs	Sheltering fishes, branching corals, <i>Symbiodinium</i> and bleaching
22. Maritorena/Washburn	CDOM production and coral bleaching
23. Carlson/Aldredge/Edmunds	Coral community structure, mucous production and community resistance

Table 2-2. List of measured or derived variables included in the MCR LTER Long-Term Time Series Program. Package ID # refers to data packages cataloged in Metacat by MCR-LTER personnel as knb-lter-packageID# (T.B.A. = To Be Assigned¹).

Variable Name	Primary Measurement Instrument / Method	Frequency	Package ID #
Oceanographic Data			
Regional Scale - French Polynesia			
Climate (Air Temp., Rainfall, Wind, etc.)	Satellites and Met. Stations – (Météo France)	Daily	T.B.A. ¹
Tides	Remote Sensing (TOPEX-Poseidon)	Daily - Weekly	T.B.A. ¹
Surface currents	Remote Sensing (TOPEX-Poseidon)	Daily - Weekly	T.B.A. ¹
Ocean color	Remote Sensing (AVHRR)	Daily	mcr.5
Light absorption/particulate backscattering	Remote Sensing (SeaWIFS)	Daily	mcr.5
Sea surface temperature (SST)	Remote Sensing (SeaWIFS)	Daily	mcr.5
Island Scale - Moorea			
Climate (Temp., Rainfall, Wind, PAR, BP, RH)	MCR and Météo France Met. Stations	Daily	mcr.9
Significant wave height and dominant period	Seabird SBE-26 pressure sensors	2 hours	mcr.30,31,32
Island-wide current speed & direction	RDI Acoustic Doppler Current Profilers (ADCPs)	Hourly	mcr.30,31,32
Water temperature	Seabird SBE-37 & 39, Onset thermistors	2-8 Minutes	mcr.30,31,32,33
Salinity	Seabird SBE-37 & 16+	2 Minutes	mcr.30,31,32
Sub-island Scale - North Shore of Moorea			
Dissolved nutrients (PO ₄ , SiO ₄ , NO ₃ , NO ₂)	Seabird SBE-19+ & Laboratory analysis	6 Months	mcr.10
POC & PON	Seabird SBE-19+ & Laboratory analysis	6 Months	mcr.10
DOC & DIC	Seabird SBE-19+ & Laboratory analysis	6 Months	mcr.10
Alkalinity	Seabird SBE-19+ & Laboratory analysis	Yearly	mcr.10
pH	Calculated from DIC and alkalinity	Yearly	mcr.10
Turbidity	Seabird SBE 19+ w/FLNTURT-221 sensors	6 Months	mcr.10
Sub-surface PAR	Rockland ALW-CMP PAR sensor	10 Minutes	T.B.A. ¹

¹ T.B.A. = Metacat data package ID # is listed as To Be Assigned. This status is reserved for data or data products archived by other agencies, universities or institutions, but that are available for use by MCR LTER researchers. Specific metadata, derived data or data products used in MCR LTER research activities will be archived in the Knowledge Network for Biocomplexity (KNB) and assigned a Metacat package ID # as needed. This status also serves as a place holder for new data or derived data products that will be collected during MCR II, but were not collected during MCR I (e.g., coral cores and sub-surface measurements of PAR).

Table 2-2. (continued)

Variable Name	Primary Measurement Instrument / Method	Frequency	Package ID #
Biotic Data			
Regional Scale - French Polynesia			
Sub-surface chlorophyll <i>a</i> concentration	Remote Sensing (SeaWiFS)	Daily	mcr.5
Island Scale - Moorea			
Reef structure	Coral cores	5 Years	T.B.A. ¹
Reef cover (large scale)	Satellite and photographic imagery	3-5 Years	T.B.A. ¹
Abundance (age/size structure of major taxa)	Transects, quadrats, photographs	Variable	mcr.1,4,6,7,8,13,15,21
Diversity (key functional groups) ²	Derived from abundance/percent cover data	Variable	mcr.1,4,6,7,8,13,15,21
Settlement/Recruitment (key taxa) ³	Transects, Settlement tiles	Variable	mcr.3, 4,16,17
Growth (key taxa) ⁴	Length/Weight measures, CHN analysis	Variable	mcr.4,20
Macro-algal nutrient uptake	CHN Analysis	6 Months	mcr.20
Sub-island Scale - North Shore of Moorea			
Primary productivity – Reef	Upstream-downstream control volume	Yearly	mcr.18,19,20
Primary productivity – Water Column	¹⁴ C tracer/bottle techniques	Yearly	mcr.10
Chlorophyll & Phaeopigments	Seabird SBE 19+ w/FLNTURT-221 sensors	6 Months	mcr.10

²Key groups include: Water column and reef associated Bacteria; Algae (corallines, turf); Corals [genus resolution - *Acropora*, *Pocillopora*, *Porites*, etc. (21 genera + *Millepora*)]; *Symbiodinium* clades; Other invertebrates (zooplankton, asteroids, echinoids, mollusks); Fishes [Acanthuridae, Apogonidae, Chaetodontidae, Cirrhitidae, Holocentridae, Labridae, Pomacentridae, Scaridae, Serranidae, etc. (~84 families)]

³Key taxa include: Algae (*Hydrolithon* spp., *Polysiphonia sparsa*, *Turbinaria ornata*); Corals: (a) recruits - family resolution (<1 mm diam) - *Acroporidae*, *Pocilloporidae*, *Poritidae*, and “others”, (b) juveniles (< 40 mm diam) - genus as in #1 above. Other invertebrates (*Acanthaster planci*, *Culcita novaguineae*, *Diadema savignyi*, *Diadema setosum*, *Echinometra matheai*, *Echinothrix calamaris*, *Heteractis magnifica*, *Tridacna maxima*); Fishes (*Amphiprion chrysopterus*, *Caracanthus maculatus*, *Chaetodon citrinellus*, *Chaetodon lunulatus*, *Chaetodon vagabundus*, *Chromis viridis*, *Dascyllus aruanus*, *Dascyllus flavicaudus*, *Dascyllus trimaculatus*, *Paracirrhites arcatus*, *Pomacentrus pavo*, *Scarus sordidus*, *Scarus psittacus*)

⁴Key taxa include: Algae (*Sargassum mangarevense*, *Turbinaria ornata*); Corals – area and length of select taxa (*Acropora hyacinthus*, *Montipora* sp., *Pocillopora meandrina/verrucosa*, *Porites rus*, massive *Porites* sp.)

Figure 2-2. (A) Spatial patterns of water column dissolved organic carbon (DOC) and bacterioplankton within the north shore reef system. DOC (right) is elevated offshore and in the bay, and is lower on the back reef and lagoon, suggesting the lagoon is a weak sink for DOC, possibly due to enhanced heterotrophic uptake of DOC. Bacterioplankton concentrations (center) are also depleted suggesting that (i) specific growth rates of lagoon bacteria are elevated to support enhanced heterotrophy, (ii) there is another, unknown mechanism that removes both DOC and free-living bacterioplankton in the lagoon, and/or (iii) that there is a unique microbial community found in the lagoon regions. Environmental gene sequences and DNA fingerprints (TRFLP of 16S rRNA genes) revealed clear spatial patterns in the structure of the bacterioplankton community (left), with unique assemblages found within the lagoon and back reef regions. **(B)** Deep 454 Pyrosequencing data confirm the TRFLP patterns of bacterioplankton community structure and suggest strong spatial structure in the presence / absence of phylogenetic groups.

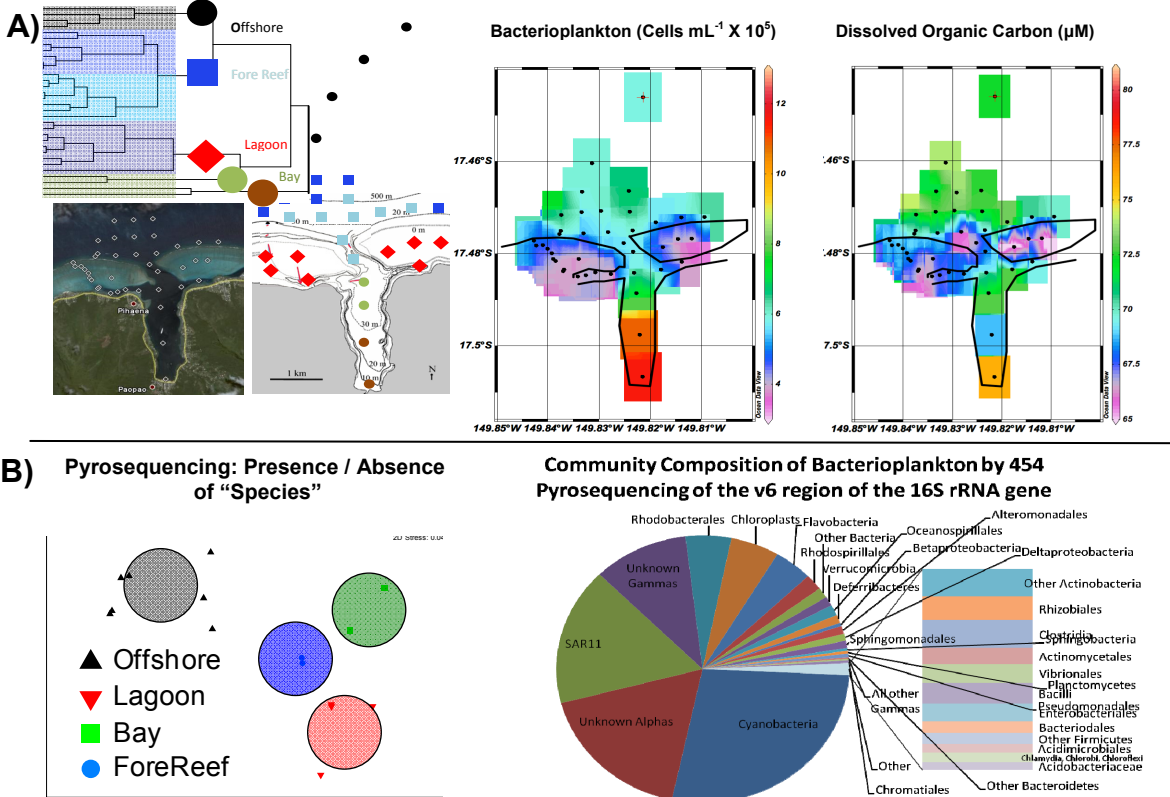


Fig. 2-3. Endosymbiotic *Symbiodinium* diversity in Moorea corals presented as a TCS haplotype network of *Symbiodinium* ITS2 sequences. Circles depict haplotypes identified by statistical parsimony (95% connection limits, gaps as a 5th state). Size of each circle indicates the number of sequences within that group, and colors inside represent the proportion of that haplotype found in the different coral genera. Lines between haplotypes indicate the number of base pair substitutions between each group (see legend for details). The network is based on 1245 ITS2 sequences isolated from 132 coral hosts representing 34 species and 14 genera.

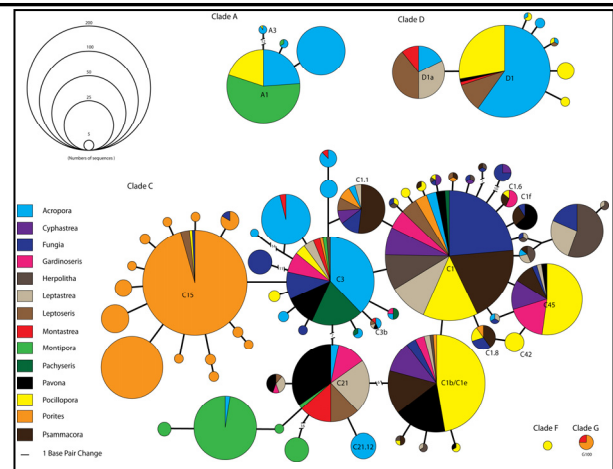


Figure 2-4. Decadal-scale trends in climate, large-scale drivers and ocean chlorophyll at Moorea. (A) – (D) are expressed as anomalies (monthly average – monthly climatology). (A) Average monthly air temperature anomalies; (B) Total monthly rainfall anomalies; (C) Average monthly Sea Surface Temperature anomalies; (D) Average monthly regional Chl anomalies; (E) Sea level at Papeete, Tahiti.

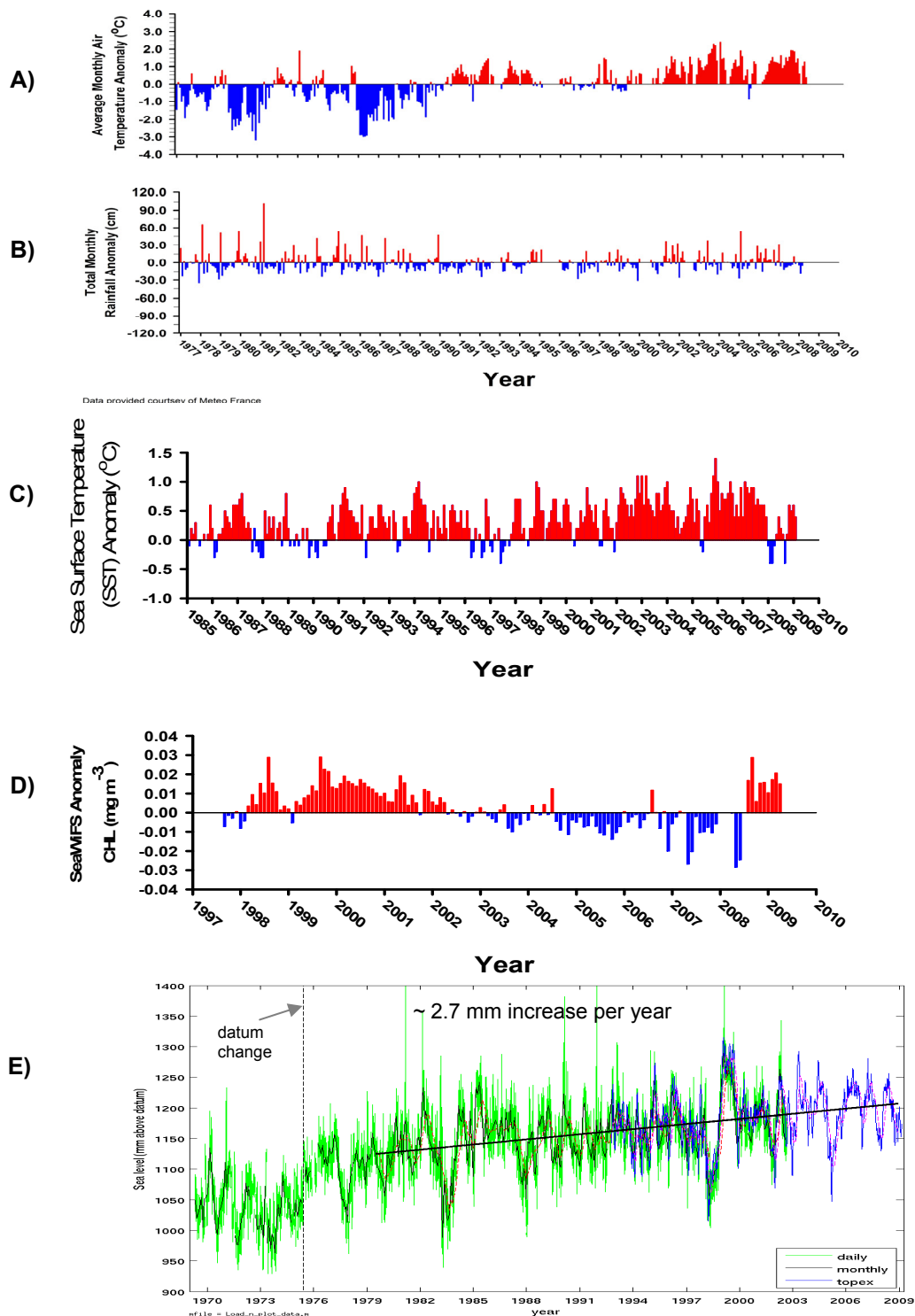


Figure 2-5. Population dynamics of a damselfish (three-spot dascyllus *Dascyllus trimaculatus*) and its juvenile habitat (the sea anemone *Heteractis magnifica*) since 1996 (representing ~1.5 – 3 turnovers of the fish population). **(A)** Inter-annual fluctuations in input estimated from daily counts (June – Sept.) of larval settlers (black circles) and multiple surveys annually of new recruits (cyan circles). **(B)** Abundances of adults (black circles) and anemones (red circles) show adults track trends in the juvenile habitat; signals from the input variance are muted by temporal compensatory mortality of juveniles (Schmitt & Holbrook 2007).

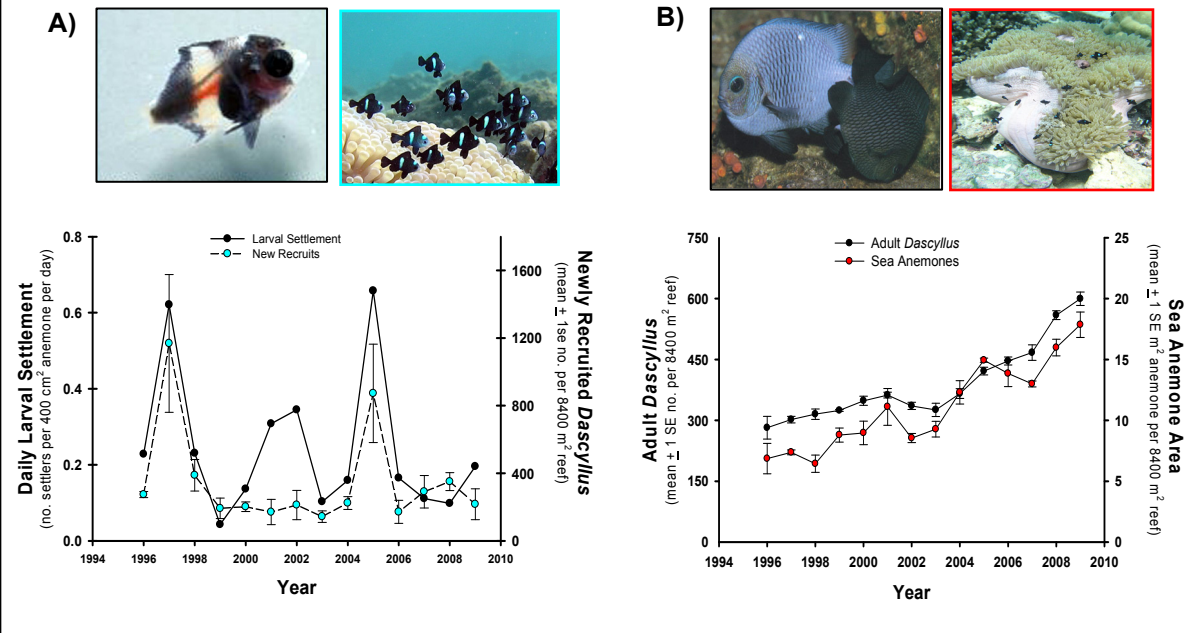


Figure 2-6. Temporal variability of internal waves, which deliver materials (e.g., nutrients) from below the thermocline, impinging on the fore reef of Moorea. **(A)** Depth stratified thermal records for the north shore over a year show strong seasonality in the occurrence of internal waves. **(B)** Detailed record for April 2005 [blue rectangle on (A)]. Strong negative temperature anomalies indicate movement of cool water up the fore reef slope.

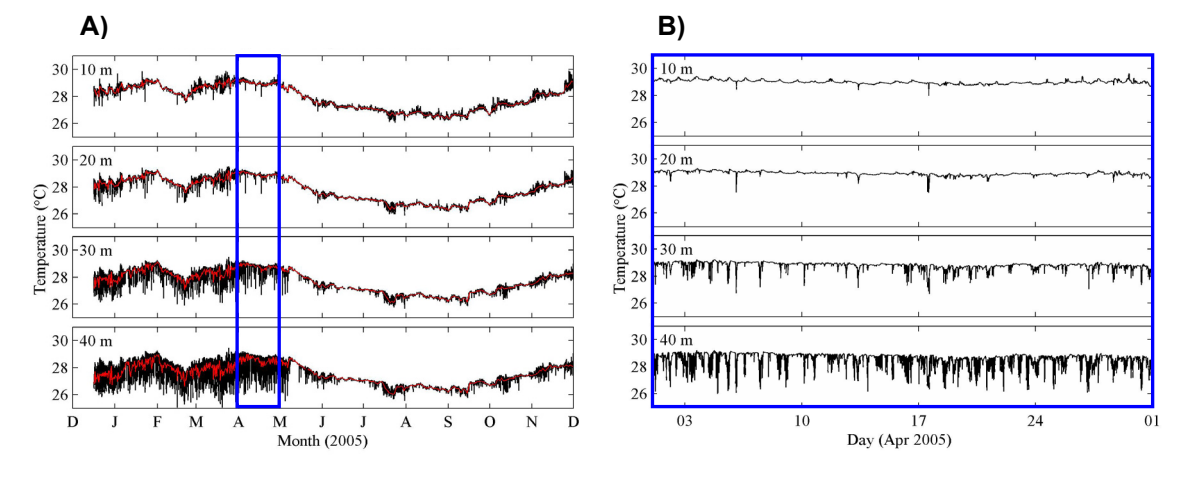


Figure 2-7. (A & B) Two scales of self-recruitment of orangefin anemonefish, *Amphiprion chrysopterus* (pelagic larval duration ~12 days) on Moorea, and **(C & D)** potential oceanographic retention and transport features. Parentage analysis of DNA fingerprints from non-lethal fin clips (photos) of 327 adults (~ 50% of total adult population on Moorea) and 104 new recruits yielded an estimate of self-recruitment at the whole-island scale of ~ 80%. For 10 recruits, we identified the specific locality of the parents in addition to the exact place where each offspring recruited. The locations of each parent - offspring pair are connected by a black arrow; six **(A)** could be explained by the shelf current **(C)**, which has a (counterclockwise) transit time around Moorea (at the 75 m isobath) of ~3-4 weeks; the rest **(B)** could be related to km-scale circulation cells **(D)** (see Fig. 1-7).

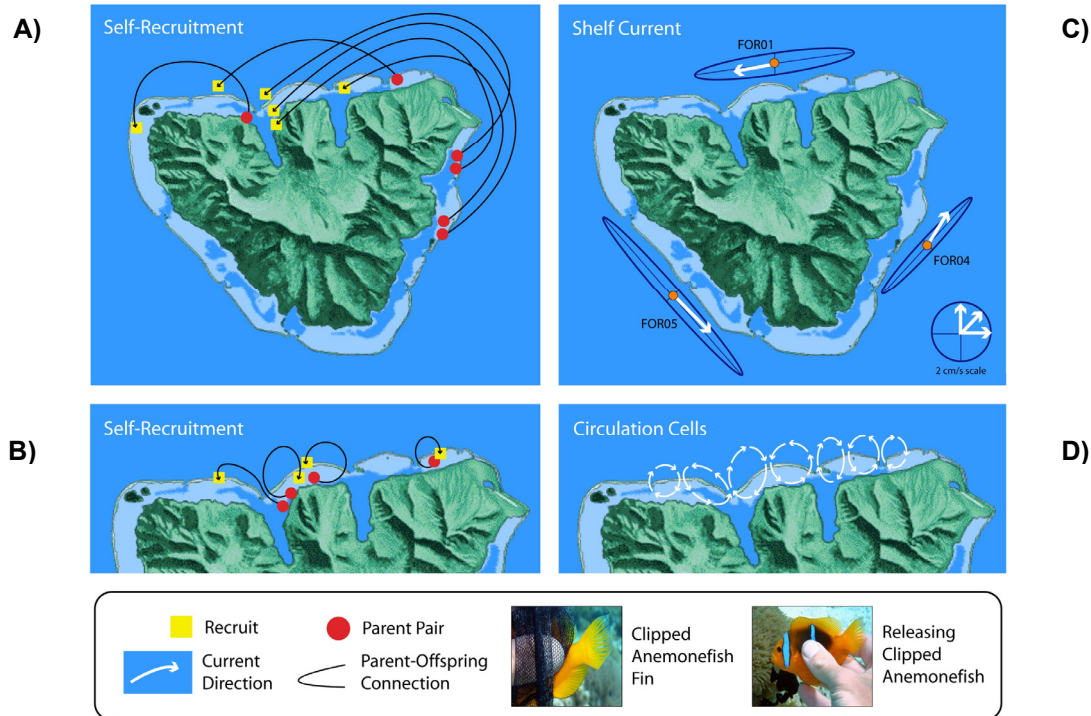
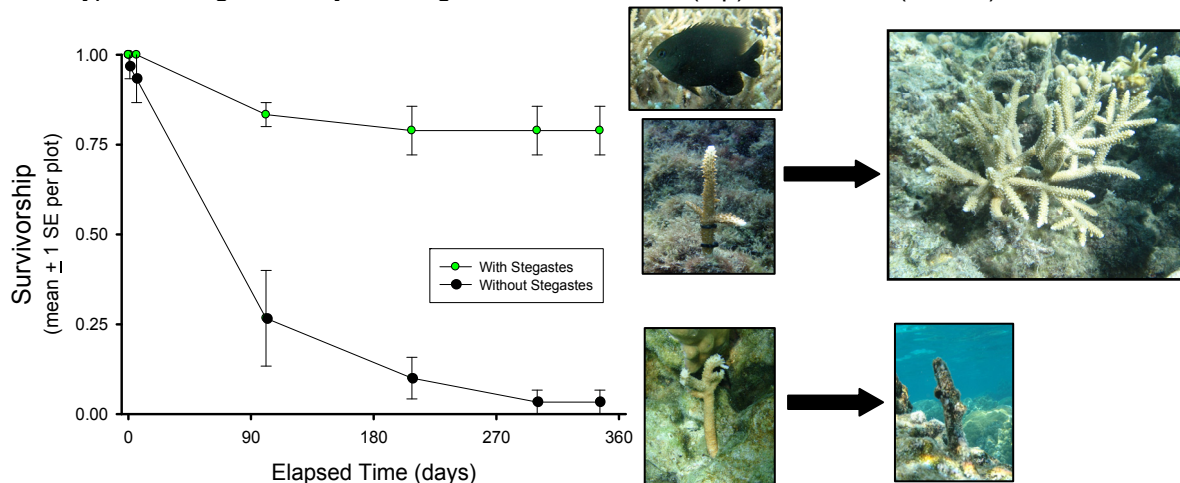


Figure 2-8. Survivorship of staghorn coral (*Acropora pulchra*) nubbins transplanted inside (green circles) and outside (black circles) of dusky farmerfish (*Stegastes nigricans*) territories. Images show typical change over 1 yr for staghorn nubbins inside (top) and outside (bottom) territories.



SECTION 3 – SITE MANAGEMENT AND INSTITUTIONAL RELATIONS

SITE MANAGEMENT

Management of the Moorea Coral Reef LTER project encompasses governance, project resource acquisition and allocation, agency, university and public relations, communication with MCR LTER personnel, and day-to-day operations (Fig. 3-1). As lead investigator, Schmitt will serve as the project's primary point of contact with NSF, the LTER Network, and campus administrative units. In close cooperation with the three Co-Principal Investigators (Carpenter, Edmunds and Holbrook) Schmitt also will oversee day-to-day operations of the project and implementation of all its components. A half-time Deputy Director (Brooks) will assist with all aspects of the project, and he also will be the liaison between the project's investigators and the Information Management team, the Education and Outreach specialist and various University committees (e.g., Diving Safety, Small Boat Safety).

Research direction, strategic planning of major tasks, initiatives, and policies will continue to be determined by consensus of an Executive Committee (Fig. 3-1) consisting of the 4 Principal Investigators plus 3 of the Associate Investigators who serve on a rotating basis. The Deputy Director, Information Manager and Education Coordinator will participate in the Executive Committee on an ex officio basis. The committee will meet once or twice a year; minutes will be archived on the MCR LTER internal server. In addition, some business will be handled by email. The Executive Committee will continue to develop and implement important policies regarding (1) data access and sharing, (2) use of MCR LTER vehicles, boats, instrumentation and mesocosm facilities, and (3) collaborative activities with groups outside the MCR LTER. These policies will be posted along with the Executive Committee meeting minutes in the appropriate locations on the MCR LTER web site.

Information transfer among researchers of the MCR LTER site is crucial because individuals are located at eight different universities, and considerable effort will go into maintaining open channels of communication and maximizing the input of all participants. Each year we will hold a 2-day MCR All-Investigator meeting at UC Santa Barbara, which will be attended by approximately 40 - 50 investigators, postdocs, graduate and undergraduate students and staff. Activities at these meetings will include research presentations and poster sessions, working group meetings for research synthesis and planning, and training sessions. The MCR LTER web site is another valuable tool for communication with both MCR personnel and other entities. The web site and data server are important vehicles for sharing project-related information, data and documents. MCR LTER research occurs at a distant research station in Moorea, French Polynesia, and our web site provides researchers with valuable information regarding travel and research station logistics and scheduling, visas, research permits, requirements for SCUBA and boating certifications, etc.

During MCR I, investigators and students self-assembled into four thematic working groups: (i) Time Series Measurements and Response of the Ecosystem to Perturbations, (ii) Coral Functional Biology; (iii) Population and Community Dynamics; and (iv) Bio-Physical Interactions and Coupling. Many individuals were members of more than one group. Working group meetings facilitated cross-disciplinary studies and promoted the inclusion of individuals of all educational stages into the project. We will continue this approach in MCR II, with three working groups organized around the major proposed research themes (Figs. 2-1 & 3-1, Tables 2-1 & 3-1), another group focused on time series measurements (Fig. 3-1, Table 3-1), and a modeling group that cuts across the themes (Fig. 3-1, Table 3-1). All investigators participate in integration and synthesis of the research program.

Planning for a long-term project like an LTER site requires a strategy for replacing expertise in research areas vacated by scientists that have left the project and

for adding expertise in areas of new research initiatives. At the MCR site, addition of new Associate Investigators is accomplished either by active recruitment to fill a specific research need, or via invitation to already collaborating scientists who are interested in becoming more formally associated with the project. In both cases the addition of new investigators will continue to be determined by consensus of the Executive Committee. Three new Associate Investigators will be added to MCR II; they include individuals from two new institutions (CSU San Marcos, Duke University). All three are early to mid-career scientists who offer a potential for a long-term commitment to the project.

INSTITUTIONAL RELATIONS

The MCR LTER will continue to be administered by the Marine Science Institute (MSI) at UC Santa Barbara. MSI is an organized research unit under the auspices of UCSB's Office of Research, overseen by Vice Chancellor of Research Michael Witherell. Administration of the MCR LTER site by the Marine Science Institute will facilitate coordination with the three other University of California campuses involved in the project, as well as with California State University (CSU) Northridge, CSU San Marcos, the University of Hawaii and Duke University. The MCR LTER also will communicate with the systemwide University of California Office of the President for input on issues related to the operations of multicampus research entities, development of MOU's and international collaborations.

The Richard B. Gump South Pacific Research Station on Moorea has been operated by the University of California for 25 years. The MCR LTER is a major client of the station and we enjoy a close and cooperative working relationship with Director Dr. Neil Davies and his staff. The Gordon and Betty Moore Foundation has provided exceptional infrastructure support to the Gump Station, including funds for laboratory facilities and housing. At the research station, MCR has approximately 1,500 sq. ft. of dedicated laboratory and office space plus a large storage facility. MCR researchers also have access to all of the additional station facilities (approximately 4,000 sq. ft. of laboratory and library facilities).

The University of California and the Territorial Government of French Polynesia have a formal cooperative agreement that the Gump Station will assist the government through research, education and outreach. All scientific researchers must hold a permit issued by the Territorial Government of French Polynesia. During the past several years, a streamlined procedure to apply for scientific research permits in French Polynesia has been employed by the Territorial Government. MCR investigators apply annually for a research permit that is issued by the Delegation for Research at the High Commission of the Territorial Government in Papeete; the Gump Station handles all of the paperwork and facilitates the process. Upon receipt of a research permit, investigators can obtain at their nearest French Consulate the appropriate visa (depending on length and frequency of research visits) to enter French Polynesia.

Figure 3-1. Management structure for the Moorea Coral Reef LTER (right), and schema for integrating components of the MCR II research program (left).

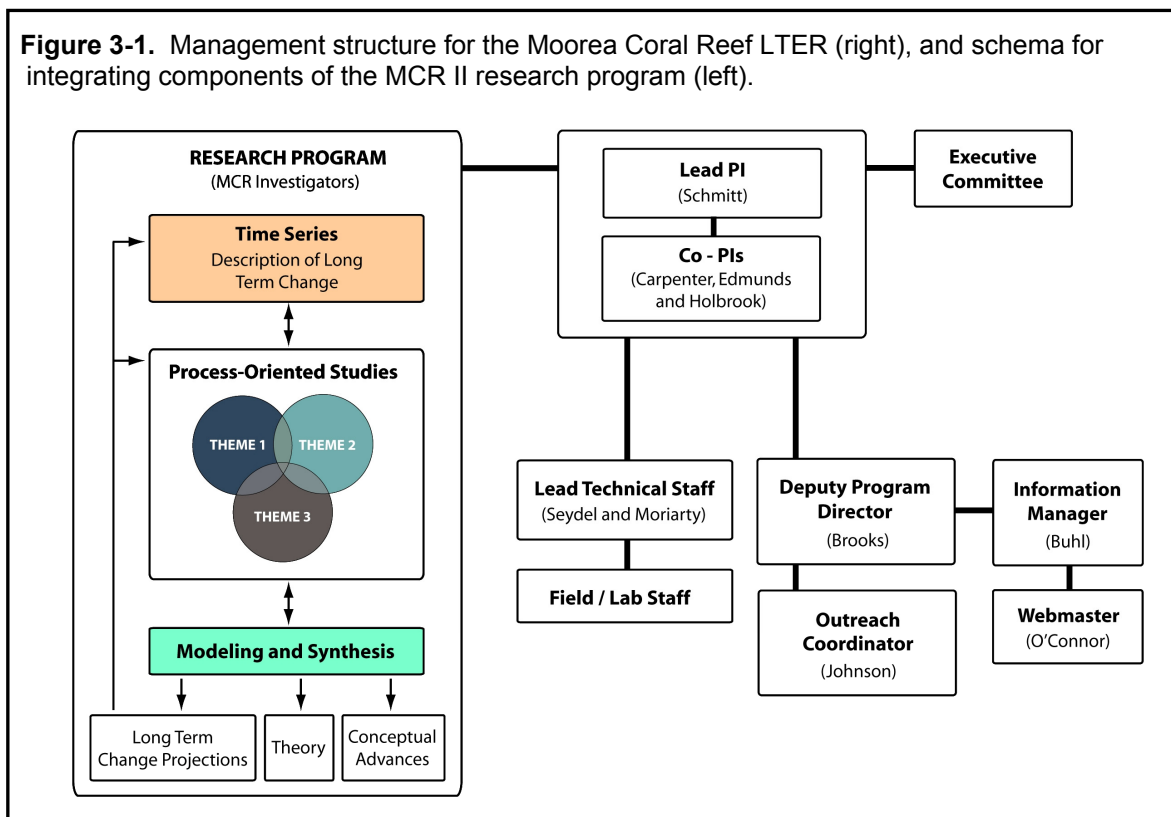


Table 3-1. Participation of MCR Investigators in various components of the MCR II research program; all MCR Investigators will be involved in synthesis activities.

INVESTIGATOR	TIME SERIES	THEME 1	THEME 2	THEME 3	MODELING
Alice Alldredge					
Giacomo Bernardi					
Cherie Briggs					
Andrew Brooks					
Craig Carlson					
Robert Carpenter					
Peter Edmunds					
Vicki Fabry					
Ruth Gates					
James Hench					
Gretchen Hofmann					
Sally Holbrook					
James Leichter					
Hunter Lenihan					
Sally MacIntyre					
Stéphane Maritorena					
Roger Nisbet					
Russell Schmitt					
Libe Washburn					
Susan Williams					

SECTION 4 – INFORMATION MANAGEMENT

INTRODUCTION

The primary Information Management missions of the MCR LTER are to facilitate the site's scientific work; ensure data integrity, security and longevity; maintain appropriate accessibility to data; and facilitate data synthesis. Information management at MCR is collaborative. The Principal Investigators, the Deputy Director, and the Information Manager work together to plan the activities and set priorities. During MCR II, improvements and new components in our Information Management System (IMS) will be driven by our missions and with compatibility in mind. This six-year renewal cycle of MCR coincides with a dynamic period of planning and development of cyberinfrastructure (CI) in the LTER network and thus provides an opportunity to further develop our local system to take advantage of these advances. MCR II activities will include:

- Participation in network efforts to optimize scientific data management
- Collaboration with other research sites to leverage or adapt compatible systems
- Support for trends toward increasingly interdisciplinary studies
- Continued commitment to comprehensive metadata in the network standard (EML)
- Modular development of the IMS to enable integration of future projects
- Ensuring data integrity and consistency throughout the data lifecycle
- Development of applications that handle data in the form of web services

STATUS AND DEVELOPMENT OF THE CURRENT SYSTEM

The MCR LTER collects diverse types of data from a variety of sources and our growing IMS reflects this heterogeneity. Highlights of the processes, tools and protocols for the MCR IMS include:

File system. The MCR file system is co-managed by the Marine Science Institute (MSI), and two other research groups: the Santa Barbara Coastal (SBC) LTER and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). MCR LTER data and document storage has three tiers of access: public access of data packages, internally shared pre-release or controlled-access data packages, and areas accessible only by the data owner. This enables us to secure new data against loss early in the process before it is ready for review and internal sharing. The file system is secured by a backup system of daily incremental and monthly full backups.

Controlled Vocabularies. MCR has robust, structured and well-controlled vocabularies for taxonomy and sampling locations. We will benefit from additional LTER and scientific community vocabularies for other data components such as keywords, observations and measurements. Where appropriate, development of vocabularies at MCR will leverage work at the network level, specifically, the LTER Unit Registry and thesaurus for keywords. Where possible, we will relate our vocabularies to existing standardized vocabularies, e.g., Global Change Master Directory, Open Geospatial Consortium.

Data Catalog. Currently 23 data packages are available publicly, both locally and through the LTER Network Metacat catalog. MCR's local data catalog is based on the XML specification adopted by the network (Ecological Metadata Language, EML), and so MCR is well placed to take full advantage of applications based on EML. Our catalog is a hybrid system that is populated from the network Metacat and transformed using local XSLT templates, which ensures that local and network searches return identical results. Currently, EML data package management, status and tasks are tracked in our database. Our practices are adequate for the present, but will not scale

up well as we expect addition of substantially more data during MCR II. We plan to survey EML management systems at other LTER sites to discover best practices as we upgrade our system. The complexity of MCR data packages varies widely; some datasets are at “Discovery” level (EML Best Practices 2004), whereas those with data tables are at Level 5 (“Integration”). Sixty percent of MCR datasets include one or more data tables. All data packages include protocols (14 embedded in EML, 9 with a downloadable document).

Web Site. MCR’s web site is a hybrid of static informational pages and dynamic pages with content supplied by our relational database. We are migrating toward an updated model, with separation of content and style and new templates implemented with W3C standards in XHTML and CSS. Migration has been gradual to minimize impact on web site users and maintainers. All web site components are stored in a version control system (Subversion, SVN). Our web site host is shared with partner projects at MSI. The security certificate is contributed by the LTER network.

NEW MODULES

We plan to take advantage of services to be offered by the LTER Network Office (LNO) as these develop (Fig. 4-1). Because computing technology changes rapidly relative to the long-term mission of the LTER network, the modular design of the MCR IM system will enable components to be replaced without requiring redesign. This design mode merges current recommended practices for programming with the pragmatic style of information management necessary for an LTER site.

Software Architecture Standardization. We plan to standardize our software architecture to a constrained group of languages and frameworks. This goal is sometimes hampered by our need to share IMS tools with other LTER sites using different architectures. Currently we use a PostgreSQL relational database as the back-end serving web site and data access. We connect to this database with a variety of languages including PHP and Java. MCR LTER will begin using eXist, an XML database as we populate our project descriptions. eXist is not a relational database, but the framework has advantages when storing, querying and displaying XML-modeled data, with built-in web services that are appropriate for the network-site relationship paradigm the LTER is developing. Several LTER site Information Managers are now using eXist, and MCR will leverage their experience. MCR will use eXist as a synchronized, redundant copy of the project data maintained in our PostgreSQL database master copy (per a similar installation at GCE). As LNO phases in synchronization of their PubDB and PersonnelDB to eXist, this will serve as the abstraction layer allowing us to grow modules asynchronously.

MCR LTER currently uses the LTER standard specification, EML, to record metadata. The Information Manager is involved in all levels of data collection. Data processing is laboratory-based in the languages preferred by the investigators and their staff. For each data product, the Investigator(s) and Information Manager discuss potential output formats, and agree on a product. In most cases the long-term data product from each lab is provided to the Information Manager as ASCII text. The exceptions are the annual biological census data, which are uploaded directly to the database by the technicians using a web interface.

Project Database Cross-Referencing. The components of the IMS are connected through the central cross-referencing in the PostgreSQL database. Here, each dataset is connected to its data products (usually tables), protocols, download links, topics and categories. Each project is characterized by its description, people, datasets, locations, publications, and reference materials. In this sense, a project can accommodate cross-

referencing between MCR Working Groups, a LTER network research focus, local research groups or labs, or even a particularly rich or diverse collaborative dataset.

POLICIES AND PRACTICES

Data Contributions and Access. LTER network policy is implemented by the MCR as follows:

- Type 0 Near-real-time physical oceanographic and meteorological raw data, and derived near-real-time event detection data are made publicly available without delay as this is part of their value.
- Type I Data that require some level of QA/QC or require some level of analysis or post-processing to generate desired data products. The majority of MCR-LTER Long-Term Time Series Program data packages are Type I, with public release as soon as data are analyzed and verified.
- Type II Sensitive data resources such those collected for use in graduate student theses and dissertations or collected in collaboration with non-MCR researchers. These data are handled on a case by case basis with special approval of the Principal Investigators and/or Executive Committee. These data will be made available to the public after an agreed to specified period of time.

Public access to data is tracked when downloaded. MCR investigators may view the record of public downloads on an internal web page. Data users accept the access policy prior to download.

Quality Assurance, Control, and Monitoring. For the majority of MCR's data components, quality assurance and control are done before submission to the IMS. Quality assurance measures built into data collection by design are encouraged. For the annual biological census data, the relational database itself constrains and validates incoming data, so that successful upload into the data model is part of the quality assurance process. Additionally, in this case a random sample of each year's data is queried and manually compared to original data sheets before the data are marked as verified. These procedures were agreed upon and designed by the Information Manager in partnership with the Investigators and their staff.

IM System Team. MCR information management is an integrated system with smooth transition from data collection to curation (Fig. 4-2). The Information Manager requests periodic conferences with each Investigator individually to review their metadata and data contributions. Areas where science may benefit from the IM system resources are identified so that the process is seen as a two-way flow. MCR site technicians participate significantly in data documentation, re-formatting, and quality control and contribute their detailed knowledge to the design of data models and protocols. The Deputy Director provides the Information Manager with site, publication and personnel information. The MCR and SBC Information Managers actively collaborate, which has provided continuity and leveraged resources since 2004.

Figure 4-1. The MCR LTER IM System, showing examples of data types and sources (ovals) and databases (cylinders). Currently only the Metacat data catalog both feeds as well as receives data and metadata, represented by a two-way arrow. The plan is for the other Network databases to be sources, not just sinks (represented by a one-way arrow). The hexagons at right represent the modular components of our web interface; the two-way arrow represents the public website queries to the IMS for content.

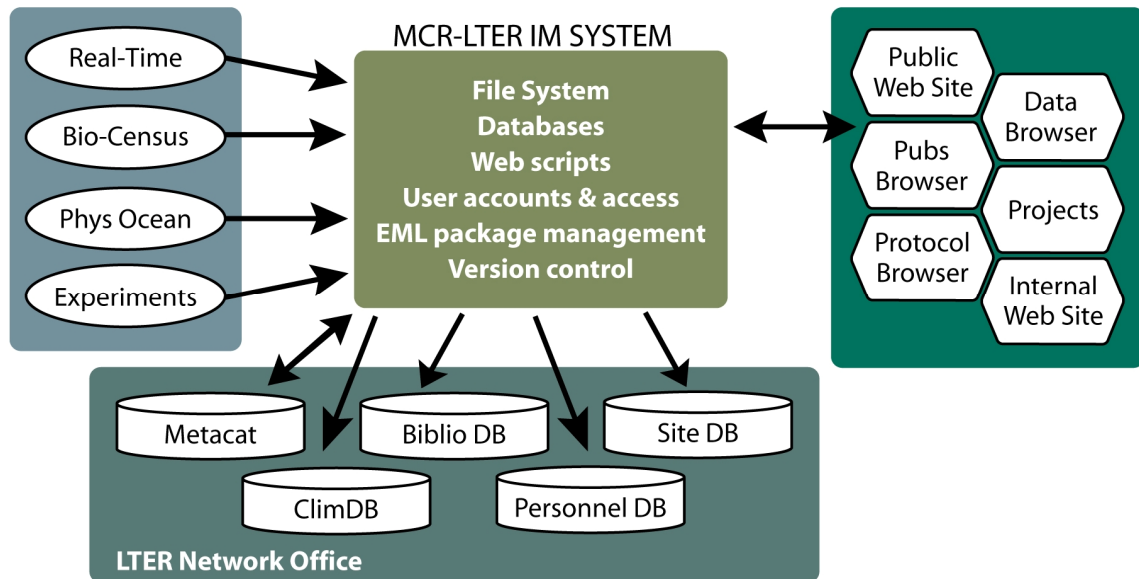
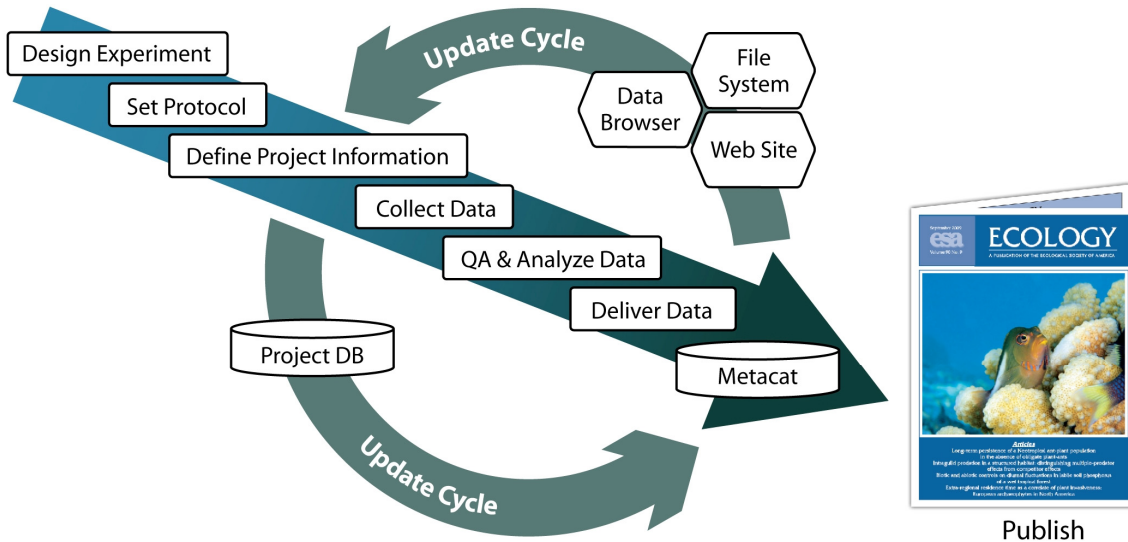


Figure 4-2. The information management process as it relates to the design and maintenance of the MCR long-term experiment. Information defined in the initial design of an experiment such as its data structure and protocols, personnel and sites are collected early in the process but regularly updated as necessary. Incremental updates of additional data collection are fed to the database (or appended to flat files on the file system) and automatically become available when new versions of metadata are submitted to Metacat. Once verified, these updates appear immediately in the public web interface to public data packages. Persistent links to protocol documents stored in the file system are linked to the metadata so that updated versions become available automatically.



SECTION 5 – DEVELOPMENT OF HUMAN RESOURCES, EDUCATION & OUTREACH

UNDERGRADUATE, GRADUATE AND POST-DOCTORAL TRAINING

Education activities include the training of undergraduate and graduate students and post-doctoral fellows. The focus at all three levels of training is to involve students and fellows directly in MCR research activities. Most conduct field work at the MCR site; others work in campus laboratories. Students of all levels participate in the annual two-day MCR All-Investigator meeting, and other site activities such as research seminars and the project's ongoing interdisciplinary working groups. Undergraduate students are involved in MCR as REU participants, research assistants on investigator projects and as recipients of mentoring by graduate students, post-docs and investigators. We will continue our investigator and student exchange program with the Kenting Coral Reef ILTER site in Taiwan; to date, 5 MCR graduate students and 1 postdoc have conducted research projects at the NMMBA at the Kenting Coral Reef site, funded through programs at NSF (EAPSI, IRFP) and NSC Taiwan (Taiwan Tech Trek) and additional MCR graduate students and one post-doc will be working in Taiwan on a recently-funded NSF grant (to Edmunds). During MCR I, we initiated collaborations with several European coral reef scientists; one MCR graduate student has already visited laboratories in France and Monaco and we anticipate additional research visits by graduate students and postdocs to take place during MCR II. In addition to integrating MCR research findings in courses we teach at our universities, we will continue to take advantage of an exceptional opportunity to integrate MCR with undergraduate and graduate instruction through the Three Seas Program of Northeastern University, a year-long marine biology course with a 10-week section taught at the Gump Station. Six MCR investigators have taught in the Three Seas Program, and several MCR graduate students serve as teaching assistants each year. MCR recently received a Research Opportunity Award that enables Dr. Joshua Idjadi, a new member of the faculty of Eastern Connecticut State University (ECSU), a small, liberal arts college, to participate in MCR research along with several undergraduate students from his institution. With ROA funding, Dr. Idjadi and his students will conduct field work in Moorea and will present results of their research at the 2010 MCR All Investigator Meeting in Santa Barbara.

OUTREACH

During MCR II, our outreach program will expand on efforts in three main areas (Fig. 5-1): (a) local outreach in California and the United States, (b) outreach in French Polynesia, and (c) web-based activities to reach the broadest possible audiences. We also anticipate completion of our children's book *Kupe and the Reef*.

(a) *Local Outreach*: We will continue our partnerships with teachers in California K-12 schools, including Washington Accelerated Elementary, Carpinteria Middle School, Kellogg Elementary School, and Viewpoint School. The NSF RET program has been instrumental in developing several of these partnerships. To date, 4 teachers have been awarded RETs to work with us in Moorea, and we will continue to pursue additional RET opportunities. We will expand our collection of inquiry-based curricula (<http://mcr.lternet.edu/education/lessonplans.html>). These units are written in collaboration with K-12 teachers (particularly our RET recipients). All lessons are aligned with the California State Science Content Standards and are refined using feedback from local teachers. We also plan to continue our partnership with the ECLC (Early Childhood Learning Center) of New Jersey, a non-profit school that provides special education for individuals with severe disabilities. We are developing lessons for 19 through 21 year old adults learning at a 3rd grade level, that incorporate sound and visual aids from Moorea into the ECLC's curriculum based on the Scholastic Inc. book "Islands" by Gordon Korman. We will be collaborating with the Coastlines Project

(<http://www.coastlines.ws/>), an NSF-funded project that has been working with the FCE and BES LTER education programs to introduce information technology concepts (GIS, GPS) to students in grades 7-12. In California, students will use data from MCR and SBC LTER to compare the two ecosystems and conduct investigations using GIS.

We will continue our outreach partnership with the Marine Science Institute (MSI) at UCSB. Our 900 gallon coral reef aquarium in the REEF (Research Experience & Education Facility) at UCSB exposes 15,000 visitors annually to MCR research. We will work with REEF staff to develop intern training procedures, maintain the exhibit, fund bus transportation for students from lower income schools to visit the REEF, and install a webcam to broadcast a live-feed of the MCR LTER exhibit. We also will develop new partnerships with UCSB's Outreach Center for Teaching Ocean Science (OCTOS), a collaboration between MSI and the Channel Islands National Marine Sanctuary (CINMS). Groundbreaking on this new facility just occurred and when completed it promises state-of-the-art, hands-on exhibits and activities.

Finally, we will continue to host a booth at the annual Santa Barbara Earth Day Festival, which drew nearly 15,000 attendees in 2009 and provided an excellent opportunity to raise local awareness about MCR research and issues related to the global health of coral reefs.

(b) French Polynesia Outreach: We will continue to work with the Atitia Center, the public outreach unit of the Gump Station (<http://moorea.berkeley.edu/outreach/atitia/>), to make MCR LTER education resources available to K-12 students and the public on Moorea through programs such as the Marine Biology Research Camp. The Marine Biology Research Camp brings classrooms of Tahitian students (ages 10-15) to the Gump Station for three days and involves students in a variety of hands-on exercises designed to provide exposure to research findings that are relevant to the local citizens. We also are working with the Atitia Center to translate our site poster and portions of the web site into French and Tahitian.

(c) Web Presence: Our web presence, through the MCR LTER Education web site (<http://mcr.lternet.edu/education/>) provides an important link between the activities of MCR researchers and the general public. We will continue to add content to the Lesson Plans and Education Programs pages of the web site, as well as adding new organisms to our Online Encyclopedia of Marine Life (<http://mcr.lternet.edu/education/encyclopedia/>). Our online content describing MCR graduate student research will grow considerably over the next six years as new students provide additional photos and "plain language" descriptions of their research. With the recent purchase of an HD video camera, we will be adding additional videos (<http://mcr.lternet.edu/education/research.html>) featuring MCR Investigators.

We plan to collaborate with the originators of the social networking web site "Whyville" to develop an MCR LTER site "pavilion" within Whyville (www.whyville.net) that users, primarily middle-school aged children, may visit to expand their knowledge of coral reef ecosystems. Whyville is an interactive virtual world focused on education and principles of online, federated learning that has an estimated 4.2 million registered users and experiences over 45 million page views per month. This pavilion will engage students in tracking long-term changes in global sea-surface temperatures, live coral cover, fish communities, and ocean pH levels.

Finally, we have initiated discussions to collaborate with the National Geographic Society (www.nationalgeographic.com) on their upcoming Ocean Initiative, which will include a series of online articles and activities designed to increase global awareness of the current state of the world's oceans and coral reefs. During MCR I, research describing how crabs promote survivorship of branching corals by cleaning sediments from their surfaces was featured on the National Geographic Kids web site (<http://kids.nationalgeographic.com/Stories/AnimalsNature/Crabs-clean-up>); we hope to make future contributions to the National Geographic Kids web site.

Figure 5-1. Examples of MCR outreach activities in French Polynesia, California and on the web.

French Polynesia Outreach



MCR Site Poster in Tahitian



Tahitian Students on a Field Trip

California Outreach

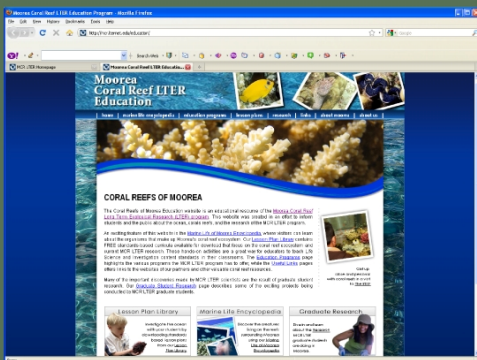


MCR LTER Exhibit at the REEF

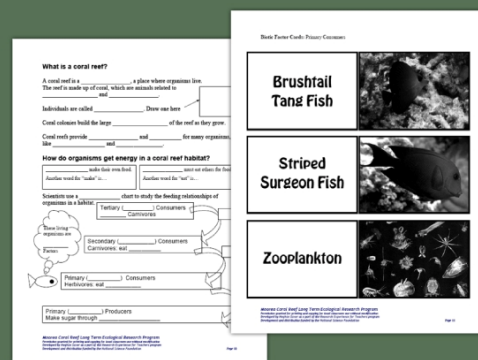


Adding to an MCR Poster at Earth Day Celebration

Web Presence



Marine Life Encyclopedia



K-12 Lesson Plans

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FACILITIES, EQUIPMENT AND OTHER RESOURCES

Laboratory:

All MCR LTER investigators have laboratory space (typically ~1,000 sq. ft. each), state-of-the-art instrumentation for a broad range of chemical and biological analyses, computing facilities and a variety of other support services at their home institutions. The UCSB Marine Science Institute's Analytical Laboratory is a professionally managed, shared-use instrumentation and chemical analysis facility that is well equipped to perform all of the chemical analyses anticipated for this project. Major capabilities of the Analytical Lab include elemental analysis of inorganic and organic substances, stable isotope ratio determination of biological materials, and automated determination of nutrients in natural waters.

Clinical:

Not required for this project.

Animal:

Schmitt, Holbrook and Brooks will maintain fishes in laboratory tanks for brief periods of time while certain field experiments are initiated in accordance with IACUC standards. The Gump Station has appropriate laboratory aquaria and ponds for studies involving fish. These tanks are supplied by fresh seawater from a once-through delivery system. The collection, care, and final disposition of fishes will be done in accordance with Federal standards as ensured by the UCSB Animal Care authority. Our animal care protocol is submitted for approval and reviewed on an annual basis. Schmitt, Holbrook, and Brooks (as well as technicians and graduate students) have completed all Federal and campus mandated Animal Care training, and they currently have an approved IACUC protocol (UCSB 2-09-639 F) for the proposed research.

Computer:

Internet service is provided to all users of the Gump Station on its secure, password protected wireless network. In addition, the MCR LTER operates two additional secure, internet connections through Mana, the local internet service provider; one connection is dedicated to data transmission from our growing real-time environmental sensor network and a second is for general internet use by MCR LTER personnel. The MCR LTER maintains 2 desktop and 2 laptop PCs for the exclusive use of MCR LTER personnel while in Moorea. All investigators in this project maintain computing capabilities at their respective institutions commensurate with their specific research activities and most travel to the field with wireless equipped laptop PCs.

Office:

In addition to office space and equipment provided to visiting researchers at the Gump Station, we have a dedicated office that has a telephone/fax machine, photocopier, dry work space, internet connectivity, and a printer. An additional 240 sq. ft. of dedicated office space is available to long-term MCR researchers and technical support staff. This space includes a printer, flatbed scanner, two general use computers and internet connectivity. All investigators have adequate office space provided at their home institutions to meet their needs and those of the postdocs and graduate students associated with this project. All offices are equipped with phone and internet services.

Other:

All field work will be conducted at the Richard Gump South Pacific Biological Station (<http://moorea.berkeley.edu/>) on the island of Moorea in French Polynesia. The Station, which is administered by the University of California Berkeley, has all of the equipment

and facilities needed to support extensive marine research. There are facilities to support scuba diving (dive lockers, Bauer 10 MiniVerticus air compressor, scuba tanks, fully equipped machine shop). Diving operations, under the auspices of the UC Berkeley Diving Safety Office (AAUS member), are conducted out of small boats within the lagoons and slightly larger Whaler-type boats for work on the outer reef slope. An NSF Field Station Improvement Grant recently supported the purchase of a new, 8 m, twin engine boat that has been modified to support offshore research. Boats may be launched from the on-site launch ramp and moored at the Station dock immediately adjacent to the SCUBA facility at the lab. The Station has a running seawater system with sufficient water tables and large outdoor tanks to support our proposed work. With funds from MCR, this facility recently has been upgraded to support (1) a tank “farm” of 15 large (750 liter) outdoor tanks suitable for holding fish and large invertebrates, and (2) an indoor wet lab designed to meet the needs of our seawater flumes, mesocosm, and indoor-wet-table needs. Additional research space includes a wet laboratory, a dry laboratory and air conditioned office space. A new, multi-use laboratory containing a large teaching lab (~25 students), smaller research labs, a molecular lab, library, meeting room, collection and visualization lab, IT center, chemical and storage rooms, and office space was completed in 2008 with support from the Gordon and Betty Moore Foundation. A small fleet of vehicles is available for general transportation. Station housing options include a large dormitory building, and seven hillside bungalows that can each accommodate 4 visitors. In addition to facilities, the Station has a permanent on-site staff of 7, which consists of a director, facilities manager, book-keeper / administrative assistant, an outreach coordinator / liaison with the Territorial Government, two maintenance men, and a housekeeper.

MAJOR EQUIPMENT:

During MCR I, the equipment context at the Gump Station changed vastly due to (a) generous gifts from the Gordon and Betty Moore Foundation (to both the MCR and the Gump Station), (b) equipment purchased through the MCR LTER grant and supplements to the award, and (c) equipment purchased by the Gump Station (e.g., through the NSF FSML program).

Over the first six years of the project, the MCR LTER built a fleet of research boats (10 total), including eight skiffs (four 4 m with 25 HP engines, four 5 m with 40 HP engines), an offshore-capable vessel (6 m with 150 HP engine), and a larger vessel capable of deploying oceanographic instruments (8 m “Safeboat” with 250 HP engine). Additionally, we purchased a Land Rover 130 pickup truck (extended crew cab), and have trailers for all boats to facilitate servicing and shore-based deployment. With the opening of the new lab building, we acquired ~1000 sq. ft. (2 rooms) of dedicated space that has been allocated equally to organismic / ecology research and molecular / physiology research. DSL/wireless internet is available throughout the building, and this will be upgraded within the next two years when the fiber optic cable from Hawaii becomes fully functional for French Polynesia. The spaces in the new building are equipped with a wide range of microscopes (graduate-grade compound and dissecting microscopes, through to a state-of-the art compound microscope), scintillation counter, water purifier, gel doc system, balances, fluorometer, spectrophotometer, refrigerator, freezer, drying ovens, muffle furnace, stabilized power supplies, tissue disruptor, centrifuge, PCR machine, and autoclave. Also, we have additional dedicated air-conditioned space for the storage of all sensitive equipment and to provide clean work space for the maintenance and programming of oceanographic instrumentation.

MCR LTER oceanographic instruments include 1 profiling CTD (SBE 19+), 1 DO sensor (SBE 43), 75 thermistors (SBE 39), 10 temperature/pressure instruments (SBE 39), 4 wave-tide gauges (SBE 26+), 10 CTDs (SBE 37), 1 CTD (SBE 16+), 4 ADCPs (RDI Workhorse), 5 ADPs (Nortek), 2 ADVs (Nortek), 1 diving PAM (Waltz), and 4 DO

sensors, 2 Li-Cor 1400 light meters in UW housings with sensors, a variety of underwater still and video cameras, and an *in situ* underwater video system with infrared illumination.

With NSF supplemental funding, we have constructed a state-of-the art Ocean Acidification mesocosm facility at the Gump Station. The facility currently consists of 12 tanks in which light, temperature and $p\text{CO}_2$ can be controlled very precisely. The system uses gas mixing technology (Qubit Systems, Ontario, Canada) to manipulate $p\text{CO}_2$ and create step-less adjustment within a range simulating atmospheric conditions expected under contemporary climate projections. The system is scalable, can support experimental volumes ranging from 2–200 liters and can be used in combination with both tanks and flumes.

The MCR LTER maintains several climate and other monitoring platforms at the Gump Station. These platforms include a research-grade weather station (Campbell Scientific) incorporating wind speed and direction, rainfall, solar irradiance, barometric pressure, relative humidity and temperature sensors and, on the reef adjacent to the Station, a Seacat SBE-16+ CTD (SeaBird Electronics) incorporating sensors for measuring conductivity, ocean temperature and ocean pressure (depth). We have installed a stationary video camera (Axis Technology Inc) with a view of Cook's Bay. All climate and oceanographic data are stored using internal data loggers (CR-1000 for weather data and flash memory for oceanographic data). Additionally, climate and oceanographic data and video are streamed in near real-time (every 5 minutes) via the internet to a DataTurbine (www.dataturbine.org) server located at the UCSD/CalIT² Data Center. Data are displayed in near-real time for the general public via the MCR LTER website (<http://mcr.lternet.edu/data/realtime>). More sophisticated data visualizations of weather, oceanographic and video feeds as well as the ability to write and execute custom event-detection algorithms and alarms are available to MCR (and other) researchers via a DataTurbine Real-time Data Viewer incorporating a Tivo®-like playback interface.

Beginning in the spring of 2010, MCR LTER site personnel will install and begin testing an experimental oceanographic mooring. This mooring will be deployed in Cook's Bay approximately 50 m from shore, directly adjacent to the Gump Station. Unlike our existing Seacat SBE-16+ CTD which is cabled to shore in order to provide streaming oceanographic data, this new mooring purchased with NSF supplemental funding will employ a Campbell CR-1000 data logger linked via an inductively coupled modem to an array of oceanographic sensors (three SBE-39 thermistors, two SBE-39 thermistors with pressure sensors, two SBE-37 CTDs, one SBE-26+ wave/tide recorder and one RDI Workhorse Sentinel Acoustic Doppler Current Profiler) and a standard 802.11 wireless receiver/transmitter to stream data in near real-time (every 5 minutes) back to a collection point at the Gump Station and then, via the internet, to the DataTurbine server at the UCSD/CalIT² Data Center. Once our initial field and reliability testing has been completed, this wireless version of our standard oceanographic mooring will replace our three existing physical oceanographic moorings. In combination with the arrival of the new fiber optic cable to Moorea and the accompanying decrease in data backhaul rates, these new wireless mooring arrays should provide MCR LTER researchers with a true, near real-time oceanographic monitoring platform deployed on the fore reef at several locations around Moorea. The bi-directional communication capabilities of these new wireless moorings will provide MCR LTER physical oceanographers with data access in near real-time and the capability to re-configure or re-task sensors on the fly from any internet access point around the world.

OTHER RESOURCES:

Major equipment available to this project owned by the Gump Station includes one 6 m Whaler-type boat with 150 HP engine, a new 8 m aluminum boat for offshore research (with 150 HP engine), and two smaller 4 m Whaler-type boats with 15 HP engines. The lab building provides air conditioned space for large group meetings/classes (equipped with AV/computer technology), additional lab space for “spill-over” projects, and office space for visitors (each hillside bungalow also has air conditioned space for office work). A wet lab facility provides access to flowing seawater pumped directly from Cook’s Bay and supplied in a cascade system to sea tables and aquaria (and our tank farm, above). The Station also has a -80°C freezer for storage of samples.

The Gump Station has a facility and personnel for the repair of small boats and outboard engines. More extensive repairs can be made in Papeete on the island of Tahiti (a 30 minute ferry ride). The Station has a small machine shop and UCSB has exclusive use of a 500 sq. ft., well-equipped machine shop, containing a table saw, radial arm saw, band saw, drill press and a full complement of small hand and power tools. More extensive fabrication requirements can be handled by commercial operations on Moorea or Tahiti. The Integrative Oceanography Division at SIO maintains an instrument calibration center at the Hydraulics Laboratory with facilities to calibrate temperature sensors and instrument compasses. Equipment necessary to fabricate and maintain buoys and drifters is provided at the Hydraulics Laboratory.

SUPPLEMENTARY DOCUMENTS

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Table S-1. MCR LTER Publications.

Journal Articles (95)

In Press

- Ainsworth, T.D., R. Vega Thurber and R. D. Gates. The future of coral reefs - a microbial perspective. *Trends in Ecology and Evolution*. In Press.
- Baskett, M.L., R.M. Nisbet, C.V. Kappel, P.J. Mumby and S.D. Gaines. Conservation priorities for coral reefs in a changing climate. *Global Change Biology*. In Press.
- Beldade, R., S.J. Holbrook, R.J. Schmitt, S. Planes and G. Bernardi. Isolation and characterization of 8 polymorphic microsatellite markers from the orange-fin anemone fish, *Amphiprion chrysopterus*. *Conservation Genetics Resources*. In Press.
- Edmunds, P.J. and H.S. Lenihan. Effect of sub-lethal damage to juvenile colonies of massive *Porites spp.* under contrasting regimes of temperature and water flow. *Marine Biology*. In Press.
- Fountain, T., S. Tilak, P. Shin, S. Holbrook, R.J. Schmitt, A. Brooks, L. Washburn and D. Salazar. Digital Moorea cyberinfrastructure for coral reef monitoring. *Proceedings of ISSNIP 2009*. In Press.
- Green, D.H., P.J. Edmunds, X. Pochon and R.D. Gates. The effects of substratum type on the growth, mortality, and photophysiology of juvenile corals in St. John, US Virgin Islands. *Journal of Experimental Marine Biology and Ecology*. In Press.
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- Leray, M., R. Beldade, S.J. Holbrook, R.J. Schmitt, S. Planes and G. Bernardi. Speciation on coral reefs: vicariance and dispersal in the three-spot dascyllus, *Dascyllus trimaculatus*, species complex. *Evolution*. In Press.
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- Price, N.N. Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia*. In Press.
- Wilson, S.K., M. Adjeroud, D.R. Bellwood, M.L. Berumen, D. Booth, Y.-M. Bozec, P. Chabanet, A. Cheal, J. Cinner, M. Depczynski, D.A. Feary, M. Gagliano, N.A.J. Graham, A.R. Halford, B.S. Halpern, A.R. Harborne, A.S. Hoey, S.J. Holbrook, G.P. Jones, M. Kulbiki, Y. Letourneur, T. Lison De Loma, T. McClanahan, M.I. McCormick, M.G. Meekan, P.J. Mumby, P. Munday, M.C. Öhman, M.S. Pratchett, B. Riegl, M. Sano, R.J. Schmitt and C. Syms. Critical knowledge gaps in current understanding of climate change impacts on coral reef fishes. *Journal of Experimental Biology*. In Press.

In Revision

- Adam, T.C. Competition encourages cooperation: client fish receive higher quality service when cleaner fish compete. *Animal Behaviour*. In Revision.
- Adam, T.C. High quality habitat and facilitation ameliorate competitive effects of prior residents on new settlers. *Oecologia*. In Revision.
- Barshis, D.J., J.H. Stillman, R.D. Gates, R.J. Toonen, L.W. Smith and C. Birkeland. Coral resistance to environmental extremes: a case for host adaptation. *Molecular Ecology*. In Revision.
- Jacobson, L.M. and P.J. Edmunds. Seawater quality over a fringing reef in St. John, United States Virgin Islands. *Bulletin of Marine Science*. In Revision

- Morris, E.D. and R.D. Gates. Differences in carbon fixation and release among zooxanthellae clades: implications for coral symbioses. *Biological Bulletin*. In Revision.
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- Yancey, P.H., M. Heppenstall, S. Ly, M. Raymond, R.M. Andrell, R.D. Gates, V.L. Carter and M. Hagedorn. 2010. Betaines and dimethylsulfoniopropionate (DMSP) as major osmolytes in Cnidaria with endosymbiotic dinoflagellates. *Physiological and Biochemical Zoology* 83:167-173.

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- Ferrier, G.A. and R.C. Carpenter. 2009. Subtidal benthic heterogeneity: flow environment modification and impacts on marine algal community structure and morphology. *Biological Bulletin* 217:115-129.
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2010

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2009

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- Goldenheim, W. 2009. The effects of flow and temperature over multiple time scales on scleractinian growth and photo-physiology in Moorea, French Polynesia. MS Thesis, California State University Northridge, Northridge, CA.
- Bergsma, G. 2009. Community effects of a coral mutualist. PhD Dissertation, University of California Santa Barbara, Santa Barbara, CA.
- Poray, A. 2009. Spatial escape at a physiological cost: consequences of coral reef macroalgae inhabiting refugia from herbivores. MS Thesis, California State University Northridge, Northridge, CA.

Spitler, M. 2009. Factors influencing the distribution and abundance of the dominant macroalgal species on coral reefs in Moorea, French Polynesia. MS Thesis, California State University Northridge, Northridge, CA.

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Muehllehner, N. 2008. The effects of increasing carbon dioxide and temperature on growth and photosynthesis of tropical corals. MS Thesis, California State University Northridge, Northridge, CA.

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Elahi, R. 2006. The interactive effects of age and size in determining phenotypic plasticity in reef corals. MS Thesis, California State University Northridge, Northridge, CA.

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Other Publications (1)

Nature – Science at the Solstice. 2006. Nature 441:1040-1045 (doi: 10.1038/4411040a)

Table S-2. MCR-LTER Data Products. Data packages are listed as currently available electronically, categorized by signature variables in the long-term monitoring program (Table 2-2). Datasets are available in several media: static files, dynamic databases, near real-time data streams and web pages. Downloads of data by the public that were requested and received (not merely browsed) are reported (509 public downloads, 84% for academic research, between May 2007 – Dec. 2009). Internal requests (by MCR investigators) are not tracked and downloads for testing purposes are excluded from these totals. Data of release Type II (restricted) are indicated as an offline medium of delivery and downloads are not tracked (nm). Download statistics for data posted since December 2009 are not given and are listed as “new”. Where signature variables in distinct categories are contained in a single package (e.g., Cruise Sampling containing Phytoplankton Primary Productivity), the download counts are listed in parenthesis to prevent double counting. Web visits to the MCR Education web pages are given for the month of November 2009.

Category		Data Package ID	Variables	Media	Public Downloads
Biological					
	<i>D. trimaculatus</i> & <i>H. magnifica</i>	mcr.2	Abundance	File	42
	<i>D. trimaculatus</i> & <i>H. magnifica</i>	mcr.3	Recruitment	File	10
	Scleractinian Corals	mcr.4	Abundance	DB	75
	<i>Symbiodinium</i>	mcr.15	Diversity, Richness	File	30
	Genetics, <i>D. trimaculatus</i>	mcr.16	Settlement, Recruitment	II	nm
	Genetics, <i>A. chrysopterus</i>	mcr.17	Settlement, Recruitment	II	nm
	Fish abundance and richness: <i>P. rus</i>	mcr.1	Abundance, Richness	File	96
	Fish census: all species	mcr.6	Abundance, Diversity	DB	66
	Benthic Algae	mcr.8	Abundance, Diversity	DB	32
	Invertebrates	mcr.7	Abundance, Diversity	DB	30
	Zooplankton	mcr.13,21	Abundance, Diversity	II	nm

II = Type II data. Type II data are obtained directly from the investigator, not through the website.

nm = Downloads not measured for Type II data packages.

new = Data became available after cut-off date (late December 2009) for which tracking statistics reported here.

() = Not included in total. Parentheses indicate variable is counted in another row.

Table S-2. (continued)

Category			Data Package ID	Variables	Media	Public Downloads
Primary Production						
		Reef: in situ upstream-downstream	mcr.18	Primary Productivity	File	new
		Reef: lab flume	mcr.19	Net & Gross Primary Production	File	new
		Reef Macro-algal CHN	mcr.20	C, H, N	File	new
		Water column: phytoplankton PP	mcr.10	Primary productivity	File	(34)
Physical Oceanographic & Meteorological						
		Remote Sensing	mcr.5	Bio-optical parameters, chlorophyll, sea surface temperature	File	27
		Mooring ADCP	mcr.30,31,32	Waves, current, temperature, salinity, turbidity	File	(20)
		Mooring CTD or Thermistor String	mcr.30,31,32, 33	Temperature, salinity, pressure	File	22
		Mooring CTD on Sensor Network	mcr.34 (new)	Temperature, salinity, pressure	stream	nm
		Cruise sampling	mcr.10	Fluorescence, turbidity, phosphate, silicate, nitrite, nitrate, POC, PON, TOC, Chlorophyll-a, Phaeopigments, bacterial abundance	File	34
		Cruise CTD	mcr.10	Temperature, salinity, pressure	File	19
		Sedimentation	mcr.12	POC, PON, sediment dry mass, sediment	ll	nm
		Met Station on Sensor Network	mcr.9	Air temperature, wind speed and direction, barometric pressure, precipitation	File stream	26
Outreach						Visits (Nov. 09)
		Education and Outreach	na	Lesson plans, Encyclopedia	web	796
		Photo Gallery	na	Photographs	web	new

Table S-3. MCR LTER-related extramural awards (excluding NSF Supplements to MCR).

Title	Funding Agency	Funding Level	Year	Principal Investigators
Science Awards				
*Ecotechnology initiative: bioengineering approaches to restoration bottlenecks	W.M. Keck Foundation	\$1,279,729	2003	Schmitt, Hu
Wave-driven flows over coral reefs and their effects on lagoon-ocean exchange	NSF OCE	\$673,716	2006	Monismith (Hench)
Building community-based research networks: global lake and coral reef ecological observatories	Moore Foundation	\$1,996,241	2007	Arzberger, Holbrook, Fountain, Kratz, Lin, Chiu
US-Taiwan collaborative research in coral reef biology	NSF OISE	\$19,999	2007	Edmunds, Holbrook
EAPSI: Coral physiological responses to temperature fluctuations	NSF OISE	\$4,579	2007	Putnam (Edmunds)
A comprehensive survey of endosymbiotic and free-living <i>Symbiodinium</i> diversity in the coral reef environments of Hawaii	NSF OCE	\$511,889	2008	Gates
Algorithm refinement for ocean color ESDR's	NASA	\$135,156	2008	Maritorena
CR: Homeostasis, stoichiometry and dynamic energy budgets at multiple levels of biological organization	NSF EF	\$712,934	2008	Nisbet, Doyle, Edmunds
EAPSI: Osmoregulation of the coral-dinoflagellate symbiosis: implications for coral bleaching	NSF OISE	\$5,637	2008	Mayfield (Gates)
EAPSI: The photophysiological response of scleractinian corals to light microenvironments on reefs	NSF OISE	\$7,000	2008	Colvard (Edmunds)
Collaborative Research: ETBC: The coupling between DOM, algae, and microbes on coral reef platforms	NSF OCE	\$1,770,673	2009	Carlson, Rohwer, Leichter, Smith
RAPID: Resilience of coral reef ecosystems	NSF OCE	\$150,000	2009	Schmitt, Holbrook
RUI-The ecophysiological basis of the response of coral larvae and early life history stages to global climate change	NSF OCE	\$626,658	2009	Edmunds
EAPSI: Nutritional Ecology of Mixotrophic Giant Clams & Implications for Fisheries Management	NSF OISE	\$8,000	2009	Yau (Lenihan)
IRFP: The effects of increased temperature and pCO ₂ on the molecular physiology of the reef-building coral <i>Seriatopora hystrix</i>	NSF OISE	\$126,120	2010	Mayfield (Hofmann)

* Awarded prior to MCR I but supported site-related research of MCR investigators and graduate students until Sept. 2006

Table S-3. (continued)

Title	Funding Agency	Funding Level	Year	Principal Investigators
Infrastructure Awards				
Moorea Coral Reef Ecological Research Site instrumentation and equipment	Moore Foundation	\$1,391,737	2004	Schmitt, Holbrook
Infrastructure improvement at the Gump South Pacific Research Station	Moore Foundation	\$2,008,974	2004	Roderick, Davies
Gump South Pacific Research Station, field transport	NSF FSML	\$109,928	2007	Davies, Edmunds

MCR LTER Postdoctoral Mentoring Plan

Training and mentorship for the postdocs to be engaged on this project will include guidance in designing and executing collaborative and interdisciplinary field and laboratory research programs. Individuals will receive training in field and laboratory techniques as well as data reduction and analysis, web and journal publication and professional presentations (including job seminars, conference talks and posters). The collaborative and interactive nature of the MCR LTER program will help to hone the specific research skills of the postdocs as well as prepare them for teaching, professional interactions and job interviews. Each postdoc will work in a specific laboratory of an MCR LTER investigator, and will participate fully in all MCR LTER programmatic activities such as the annual MCR All Investigator Meeting, regular working group meetings, and seminars. There will be ample opportunity to present research findings and receive feedback. In addition, postdocs will be encouraged to participate in LTER Network-wide activities, such as the All Scientists Meeting, workshops and working groups, and training programs, as appropriate. The postdocs also will work with graduate and undergraduate students, providing them with an opportunity to improve their mentoring skills. Guidance will be provided in preparation of new research proposals. Additional aspects of mentoring include advising about long-term employment options and opportunities, facilitation of professional networking, and providing research opportunities such as visiting other labs, trips to scientific meetings and to research sites.